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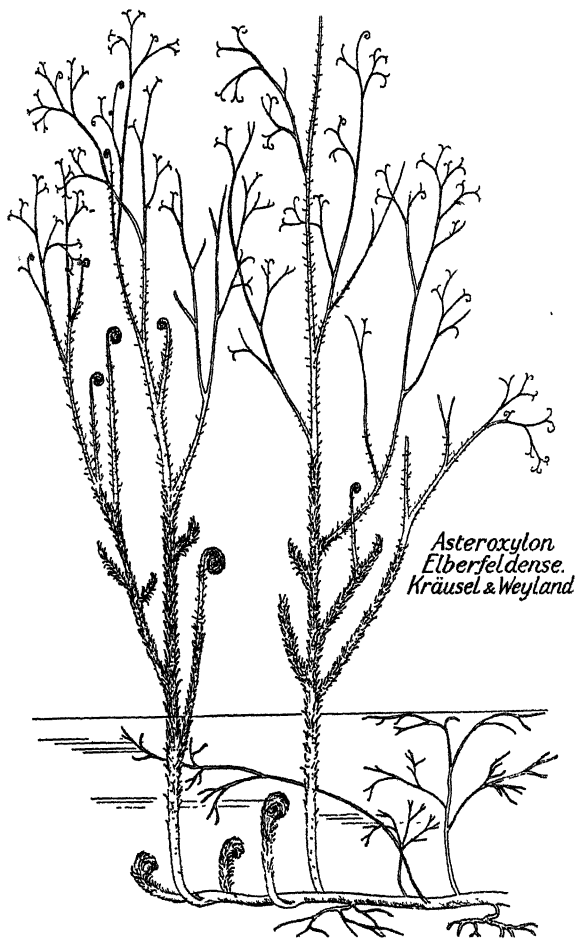
PRIMITIVE LAND PLANTS



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Reconstruction of the whole plant of *Asteroxylon Elberfeldense*, Kräusel and Weyland, from slabs collected at Kirberg.

The horizontal rhizome is naked and creeping, with many irregularly dichotomous branches. The thicker upright shoots are circinate while young, and leafy: when mature they are about 1 metre high, showing sympodial dichotomy. In the more delicate, freely branched and distal *Hostimella* region leaves are absent, while sporangia have been seen to be borne on the ultimate twigs. After Kräusel and Weyland.

PRIMITIVE LAND PLANTS

ALSO KNOWN AS

THE ARCHEGONIATAE

BY

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WITH 465 ILLUSTRATIONS

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TO THE MEMORY OF
DUKINFIELD HENRY SCOTT,
WHO STUDIED FOSSIL PLANTS
IN THEIR RELATION TO THOSE NOW LIVING,
THIS ESSAY
ON LIVING PLANTS AS ILLUMINATED BY THE FOSSILS
IS DEDICATED
BY HIS FRIEND THROUGH MORE THAN HALF A CENTURY,
THE AUTHOR.

PREFACE

The Origin of a Land Flora was published in 1908. The present volume deals twenty-six years later with the same problem, but it is in no sense a second edition of the earlier work. Nevertheless many illustrations and some excerpts from the older text have been embodied in this, though it is essentially a new book. The same general attitude to alternation is here retained as in 1908. The sporophyte is still seen as a somatic diplophase interpolated between syngamy and reduction, while the conditions of amphibious life are believed to have stabilised it when once it had been produced. The former work dealt almost exclusively with the diplophase: here both this and the haplophase are brought into the discussion: but naturally, as the diplophase becomes dominant, the greater weight in comparison will fall upon it.

Up to 1908 the opinion was current that the greatest gap in the comparison of early vegetation of the land lay between the "Mosses" and the "Ferns": and the *Land Flora* was written with that in view. But the discoveries, dating from 1916 to the present day, of hitherto unknown fossils from early horizons, have transformed the problem by the demonstration of types which can hardly be read otherwise than as synthetic. They appear to link the Bryophyta and Pteridophyta into a related sequence, while the Bryophyta themselves have now been recognised as of Palaeozoic age. Meanwhile comparative study has revealed rather than closed the gap between any known Algal type and any sufficiently known Archegoniate plant. So far as living plants are concerned, that gap appears as wide to-day as it was in 1908.

The discussions on alternation summarised in the *Land Flora* have already marked a transition from a purely morphological to an organographic treatment of the problem. The conditions affecting the development of plants on dry land were there taken into account, and it was shown that the origin and stabilisation of an advancing diplophase were events biologically probable. But in common with all organographic writing of the time, the influence of Size as affecting Form in primary development was ignored: nevertheless we now see in this an all-pervading and inevitable factor that cannot be excluded by experiment, though the effects produced by all the rest may be modified, controlled, or even inhibited.

The individual soma of the Archegoniatae, whether haploid or diploid, normally enlarges upwards, and its primary form becomes more or less *obconical*, a fact shown conspicuously by many illustrations in this book. Provided the original form be retained, it follows, from the Principle of Similarity, that as primary growth proceeds there would be a lessening proportion of the limiting surfaces, whether superficial or internal, to the bulk they enclose, such as would lead to physiological disability. This may be relieved by any change in Form, and elaboration of Form does habitually follow increase in Size. This suggests some power of self-adjustment—individual or racial, or both—tending to maintain a due proportion of surface to bulk. The expression "Size-Factor" has been used to designate that power, which leads to increasing complexity of Form as the Size itself increases. Once this morphoplastic factor is recognised, no problem of *primary development* can be fully investigated without taking it into account. But in relatively advanced types the primary development is apt to be overgrown and obscured by secondary advances due chiefly to intercalary growth and cambial activity. It is here that the Archegoniatae possess a special organographic interest: for in them the primary features are better displayed and developed, along the lines of advancing size, than in other land-living plants.

A third innovation since 1908 has been the introduction of the Telome Theory of Zimmermann. It follows naturally from that closer comparison of the Bryophyta with the early Pteridophyta which has been promoted by intensive study of the Devonian fossils. Nothing in the recent history of Morphology has contributed so much as this new knowledge of early vascular plants to consolidate the upward scale of the Land Flora. Zimmermann's terminology brings a new aspect into its study, rather than any new method or system. The spore-bearing unit is thus crystallised out from the general medium of fact and comparison, and the building up of the more complex types of primitive vegetation, as forms variously derived from the simple unit, is naturally suggested. This helps to confirm the upward evolutionary vision as against the downward analysis of an earlier period.

Other publications produced since 1908 have greatly influenced the organographic outlook upon early vegetation. Successive editions of Von Goebel's *Organographie* have brought a wealth of new facts, criticisms, and conclusions, of particular value in balancing reduction as against advance. It will be found in the chapters on the "Bryophyta" how deeply the author is indebted to that great work. Much new matter relating to the Algae has also appeared from the hands of Oltmanns, Svedelius, Knight, and others: bringing accessions of fact, combined with generalisations from them, which have thrown welcome light upon the problem of alternation.

New aspects of the main question here at issue have thus been worked into the text of the present volume. Their introduction has led to a change of plan, as compared with the earlier book. The material has here been divided into Two Parts. The First Part includes Chapters I.-XXIII., in which the several Classes of the Archegoniatae are described and illustrated, and within the nearer limits of natural affinity compared. The Second Part includes Chapters XXIV.-XXIX., each of which is devoted to the discussion of some one feature common to all : such as Alternation, Embryology, or Spore-Producing Members. In Chapter XXX., a general organographic analysis of the Archegoniatae has been offered ; and finally, in Chapter XXXI., a summary of results and conclusions. The scheme of the book is thus inductive, and the course of the treatment progressive from what is believed to be primitively simple towards what is more recent, and often more complex. An upward outlook is preserved throughout, but tempered by admitting reduction wherever it appears to be reasonably probable. A due sense has also been retained of the known biological conditions from which progress or retrogression have followed. Moreover the results have been held subject to the positive check of palaeontological fact which, with its greatly extended record, is more effective to-day than at any previous period in the history of the Science.

While the numerous references made to current writings proclaim indebtedness to many colleagues and friends, no attempt has been made to give a full citation of the extensive literature relating to Primitive Land Plants. But opportunity has frequently been taken for showing where, in the books and memoirs quoted, fuller references may be found. In addition to these obligations I wish specially to acknowledge help received by advice and criticism, as well as by supply of the originals of certain illustrations, from Professor W. H. Lang of Manchester. In certain references to the Animal Kingdom I have been aided by Professor Graham Kerr, to whom acknowledgment is due. And I am particularly grateful to Dr. S. Williams for various suggestions, and for his care in reading the proofs : thus an added freedom from textual errors has been secured. But for the opinions expressed responsibility lies wholly with myself.

F. O. BOWER

RIPON, *September*, 1934

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PRIMITIVE LAND PLANTS, ALSO KNOWN AS THE ARCHEGONIATAE

INTRODUCTION

THE Archegoniatae comprise in general terms the Mosses, or Bryophyta, and the Ferns, or Pteridophyta. In the nineteenth century these plants were often styled the "Higher Cryptogamia." In a more extended sense the Gymnosperms might also be included. The feature which they all have in common is that the female organ of propagation is an *archegonium*. This organ may vary in its position, its proportions, in the details of its structure, and in the steps of its development. The essential point of its

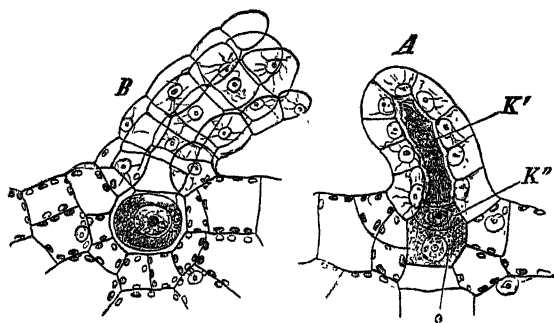


FIG. 1.
Archegonia of *Polypodium vulgare*. A, still closed. o=ovum. K'=canal-cell. K''=ventral canal-cell. B=an archegonium ruptured. $\times 240$. (After Strasburger.)

construction is that an internal row of cells, of which the innermost is the *egg* itself, is completely protected by a sheath of living cells up to the time of its maturity. But when the archegonium is fully ripe a channel is opened by rupture at the apex, giving free access to the egg from without, though it is still fully enveloped otherwise by living tissue (Fig. 1). The constancy shown in these essential features, notwithstanding the variety in detail of the whole organ, is a very striking fact of observation. The archegonium is a nursing organ for the egg, and still more for the embryo which it produces after fertilisation. The protection thus afforded enables the egg and the embryo to survive, though the whole organ be exposed to air that is not saturated

with moisture. The prevalence of the archegonium in primitive types of land-vegetation shows the importance of such protection for the otherwise vulnerable egg, or the embryo: it contrasts with what is seen in Algae, where the eggs are often discharged into the water in which they live as naked spheres of protoplasm. Archegoniate plants with their eggs thus protected are prevalent in moist situations. Cognate forms also make up the majority of the fossils found in the primary rocks. These facts raise interesting evolutionary questions in reference to the Origin of a Land Flora.

At the outset such general questions will not be discussed, save occasionally in relation to certain details as they arise in the descriptive part of this work. The first aim will be to present a picture of the several types of living organisms which are included under the term Archegoniatae, with suitable allusions to their fossil correlatives. We shall then proceed to discuss the bearings of the facts acquired from a comparative and evolutionary point of view: and so approach some rational opinion as to the origin of a Land Flora, and a recognition of the principles which underlie Form in the several types of plants that compose it. As an introduction to the descriptive section of this work a brief historical sketch may not be out of place. Its object will be to show the steps by which the present position of comparative morphology has been reached, and to reflect the changing outlook of botanists upon this peculiarly interesting phase of the vegetation of the Earth.

The earlier botanists observed little more than the external form of the adult, taking note in a somewhat desultory way of the more obvious of the propagative organs that they bear. A deficiency at first in the means of magnification, and a want of skill in preparation even after the microscope had been brought into use, sufficiently explains the absence of that closer observation which is essential before comparison can proceed beyond crude initial steps. It will be needless here to detail the slow progress of the study of the Archegoniatae, or "Higher Cryptogamia" as they were then called. That very name sufficiently conveys the fact that little was known of their propagation before 1840. Though sexual reproduction was assumed to exist generally—that assumption being often based upon acute reasoning from imperfect data—still the actual facts were hidden from the eyes of the early observers. But the improvement in microscopic technique which accompanied the pioneer work of the phytotomists of the eighteenth century naturally led onwards from the study of the cell-walls, which chiefly engaged their interest, to an exact observation of the protoplasmic body. We might date almost with precision the birth of the newer science of comparison, which is based on protoplasmic detail, from the introduction of the word "protoplasm" by Von Mohl in 1846, and the realisation by him of what it connotes (*Bot. Zeit.*, 1846, p. 73). The coining of a word may stamp though it does not itself originate an innovation of thought. As a matter of fact a recognition of the presence and importance of the protoplast was not sud-

denly but gradually attained. Von Mohl himself had by observation taken his full share in the achievement.¹ He described and depicted the "primordial utricle" (*Bot. Zeit.*, 1844, p. 273). Already in 1831 Robert Brown had recognised the nucleus as a recurrent feature in the cells of Orchids, while Kützing, Karsten, and Schleiden had each contributed his share of detailed observation. But it remained for Von Mohl to state the general position thus: "In the centre of the young cell lies the so-called *nucleus cellulae* of Robert Brown. The remainder of the cell is more or less densely filled with an opaque viscid fluid of white colour—which fluid I call *protoplasma*." In the words of Sachs (*History of Botany*, Engl. Edn., p. 313), "It was soon perceived that cell-formation in the Animal Kingdom agreed in the main with that of the Vegetable Kingdom, as Schwann and Kölliker had intimated in 1839 and 1845." Such knowledge of the protoplasmic system of the living organism was essential before the life history of any archegoniate plant could be followed through the sexual phase, for this involves naked protoplasts temporarily independent of the investing wall.

By the full recognition of the protoplasm and nucleus the stage was prepared for the entry of Hofmeister. Methodical collation of newly acquired facts enabled him to demonstrate for many archegoniate plants, whether Bryophytes or Pteridophytes, that essentially the same cycle of events underlies the life-history of each: in fact that, though differing widely in form and proportion, two generations alternate one with another, the phases being respectively sexual and non-sexual. His collected results were stated in the *Vergleichende Untersuchungen*, published in 1851. An English translation, produced by the Ray Society in 1862 under the title of the *Higher Cryptogamia*, included also his cognate researches on the Coniferae. This great synthesis, which brought alternation to the front, has proved itself to be the foundation for all subsequent morphology of land-living plants.

While we admire and appreciate the impressive results attained by Hofmeister, we should not forget that work of the highest significance was being done upon the Algae during the same period. It may not at the time have appeared to bear the same constructive value as that upon the Archegoniatae: but as in the search for origins we probe ever downwards, these results are now being evaluated afresh. In Germany many workers, particularly Nägeli and Pringsheim, were following the successive stages in the life-stories of various Algae. In France the work of Bornet and Thuret, from 1846 onwards, resulted in the sumptuous *Études Phycologiques* of 1878. Such researches ran parallel in time and in spirit with those of Hofmeister on the Archegoniatae. It has taken three-quarters of a century to interpret these results in terms of the nuclear cycle. But in the researches

¹ For the history, as told by Von Mohl, see *Die vegetabilische Zelle*, 1850; translated by Henfrey under the title *Mohl, on the Vegetable Cell*, London, Van Voorst, 1852, p. 36, etc.

of Nägeli and Pringsheim, and of Bornet and Thuret, we find many of the basic facts upon which rests the present knowledge of the Algae. It is now known that in many Thallophytes a life-cycle exists fundamentally similar to that of the Archegoniatae.

In 1859 came Darwin's *Origin of Species*; and that degree of uniformity of the life-cycle which had been demonstrated for the Algae and Archegoniatae appeared to fit readily into the frame of evolutionary theory. The general position thus attained was soon after summarised in the Text-book of Sachs, which ran through several German editions before it was translated into English and published by the Oxford Press.¹ No book of the middle of the nineteenth century had so profound an influence upon special morphology as it appeared at that period to botanists in general. The wider knowledge of life-histories acquired as time went on, and particularly those exceptional divergences from the normal succession of events, described in individual cases from 1874 onwards under the names of apogamy and apospory, led to discussions as to the evolutionary origin of the prevalent alternation of generations. Divergent views on this were associated respectively with the names of Pringsheim and Celakovsky. These will be discussed in a later Chapter (XXIV). But at the time the cytological facts necessary for a settled opinion were not available. Meanwhile the technique of microscopic preparation was advancing rapidly. By its aid enquiry was focussed upon the behaviour of the nucleus in division. This special study was initiated for plants by Strasburger, who, together with many others, concentrated upon the processes of propagation. Such enquiries culminated in a general statement by Strasburger on "The Periodic Reduction in the Number of Chromosomes in the Life-History of Living Organisms," made before the British Association at Oxford in 1894.² Thus the alternation of generations recognised by Hofmeister was at length shown to be based upon a cytological foundation which presents analogies with the propagative processes seen in animals, though in them no such alternation exists.

In 1908 *The Origin of a Land Flora* was published, with the second title, "A Theory based upon the facts of Alternation." A working hypothesis was there offered that the Archegoniatae sprang from green aquatic forms, of shallow fresh water or of the higher levels between tide marks, where the sexual propagation could be effected through the medium of external water: and that certain forms established themselves on land, where access to external liquid water was only an occasional occurrence. Thus less dependence could be placed on sexuality for propagation, and an alternative

¹ 1st Edn., 1875; 2nd Edn., 1882; Goebel's *Outlines*, based on Book II of the Text-book, 1887.

² *Annals of Botany*, vol. viii., Sept. 1894. *Biol. Centralbl.*, Band xiv., p. 817, Dec. 1894.

method of increase would be advantageous. This was effected by the advance of the sporophyte, so that the egg once fertilised might divide, producing numerous carpospores: and dry conditions would favour their dispersal. Increase in their number entails increased nourishment, hence the sporophyte would assume the nutritive function, with sterilisation of potential spores as a step to that end; and finally appear as a plant with stem, leaf, root and sporangium. Given a conservatism in the mode of fertilisation, the rise and progress of the archegoniate sporophyte would appear to be a natural outcome of amphibious life. On the other hand, before the end of the century Potonié had referred the leaves of the higher plants in origin to segments of a thallus such as may be seen in the larger Brown Seaweeds. A similar general conception was developed later by Church in his essay on the *Thalassiophyta*.¹ He specified, as Algae of Transmigration from water to land, highly organised seaweeds three to six feet long. These divergent ideas will be discussed later. They are mentioned here to show how widely theoretical views may differ where the facts are deficient. The gap between any known Alga and any Archegoniate plant was, at the opening of the present century, still too wide to allow of any comparison that could be held as close or cogent. In default of consecutive fact the enunciation and support of any theory must needs depend upon balance of probability, and the balance may be variously struck by different minds.

With the year 1916 a new era of observation opened, and the facts since disclosed tend to fill in the early record of Archegoniate life on land. Fossil Plants of Devonian time had long been known; but new discoveries, many of the specimens showing very perfect preservation, have consolidated knowledge of the earliest Land Flora of which there is any direct record. For the most part these plants were found to correspond in essential features with Dawson's old genus *Psilophyton*, and are now ranked in a new Class of the Psilophytales. First there appeared, in 1916, Dr. Halle's description of Lower Devonian Plants from Rörägen in Norway.² Since then we have been presented by Kidston and Lang with a realistic picture of an early Devonian Flora based upon very perfect preservation of certain of its constituent plants (*Trans. Roy. Soc. Edin.*, 1917-1921); and this has been supported and enriched by the discoveries of Kräusel and Weyland from the Rhine valley (*Beitr. Kennt. d. Devonflora*, 1923, etc.). The nearest living correlatives of the Psilophytales are to be found in the genera *Psilotum* and *Tmesipteris*; and it happened that, almost coincidently with this new knowledge of the fossils, the prothalli of both these genera were described in detail by Lawson, and by Holloway: moreover, the latter author followed through the embryology of *Tmesipteris* (*Trans. N.Z. Inst.*, Vols. L, LIII).

¹ Oxford Press, 1919.

² K. Svensk, *Veten. Hand.*, Bd. 57, Stockholm.

All such facts, which are mentioned incidentally here, will be described more fully later. They tended to fill in that dearth of reliable detail which had hitherto obscured the most primitive of the known plants of the land. The blanks are still ominous. There is no knowledge of the gametophyte of the Psilophytales. We only infer from comparison that they possessed an alternating generation. Our knowledge of most fossils is in this respect incomplete as compared with the observation of the whole cycle, which has now been traced for all the leading types of the living Archegoniatae. This deficiency, which can only be met as yet by inference, must be set off against the positive value which attaches to the demonstration that such types existed at so early a date as the Lower or Middle Devonian Period.

It will be gathered from this brief historical sketch that comparative morphology of the Archegoniatae stands at the moment at a critical point, and any conclusions will continue to be open to revision so long as there is an influx of new facts such as recent years have yielded. The questions for ultimate discussion will be not only the origin of the Archegoniatae, and their probable relation to the Thallophytic Flora, but also the degree of their affinity with seed-bearing plants, and the part which they have themselves taken in the establishment of a Land Flora. In order to base the discussion of such questions upon a sound footing it will be necessary to enquire how far the features brought into comparison are themselves determined by the conditions, and are results of relatively immediate homoplastic response, rather than ancient features rightly held as indices of relationship. There is reason to believe that in the past this question has not been sufficiently considered. It is certainly the fact that the systematic grouping of Ferns has had to submit to frequent revision on such grounds.

Before these questions are taken up the essential facts upon which opinion may be based must be advanced. Nor should the discussion of them be prejudiced in the statement by premature expressions of opinion. Accordingly, the earlier Chapters (I-XXIII) will be devoted to exposition of fact rather than to general comparison: while this will be in the main reserved for the present, and taken up in the concluding Chapters (XXIV-XXX).

Nevertheless, one fundamental generalisation may be here stated, which applies normally for all organisms which show sexuality; in particular it will be found to underlie the whole special study of the Archegoniatae. It is that there is in each normal life-history a cytological cycle, which may be represented diagrammatically as in Fig. 2. Two critical events follow one another as a rule in regular succession, viz., *Syngamy*, by which the number of chromosomes is doubled as a consequence of the fusion of two nucleated gametes, producing a *diploid state* in the resulting zygote; and *Reduction* or *Meiosis*, by which on tetrad-division the number of chromosomes is halved, and the original number re-established, giving a *haploid state*. Either the haploid phase (x) or the diploid phase ($2x$) may be unicellular and

remain so ; or either may undergo vegetative division, by which the chromosome-number is not changed, to form many similar units. If these separate after division the phase or "generation," though repeated, remains unicellular. If after vegetative division the products cohere, a *soma* or pluricellular plant-body is constituted. Thus in the course of evolution there are in each completed cycle two periods when somatic existence may have been established : one between reduction and syngamy, which is haploid, and is called the *gametophyte*, or *haplophase*, and it is *sexual* ; the other called the

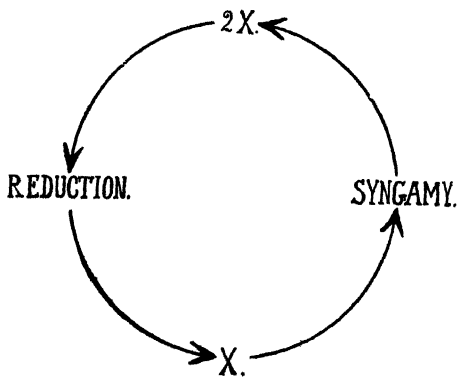


FIG. 2.

sporophyte, or *diplophase*, between syngamy and reduction : it is *diploid*, and *non-sexual*. The prevalence of this succession of events justifies its acceptance as *normal*.

Two further observations of general import may be made with regard to these alternating somatic phases. First, that their balance of size or complexity may vary, the differences being doubtless related to the conditions of life. This is illustrated by the fact that in the Bryophytes the gametophyte is preponderant as compared with the sporophyte, while the balance is reversed in the Pteridophytes. But this in no way affects the relation of the alternating phases in the cycle as a whole. The second is more open to controversy, viz., that notwithstanding such frequency of departure from the constancy of alternation as is seen in the phenomena of apospory and apogamy,¹ it cannot be assumed that in the descent of the Archegoniatae the generations were themselves irregular or indefinite. No stable evolutionary lines are known to have been established in natural circumstances, and propagated as definite races of the Archegoniatae, in which such instability is inherent so as to provide a systematic character. This is believed to show that that underlying succession of events, which is held as normal for the archegoniate plants living to-day, has been normal also for

¹ See chap. xxiv., pp. 487, 495 ; also Bower, *Ferns*, vol. i., chap. xvi.

their ancestors throughout descent. *In fact, that a regular alternation has been and is fundamental for the amphibian life of the Archegoniatae.*

The preceding paragraphs will have conveyed for the convenience of readers the general point of view to be entertained in this work. They should suffice to prepare the way for an exposition of the facts upon which the comparisons of the later Chapters are to be based. In the detailed statement of those facts the arrangement here adopted must not be understood as indicating any definite opinion as to the kinship of the several phyla described. Nevertheless, opinions may from time to time be expressed as to the inter-relations of the plants which constitute individual phyla. To any one who may entertain a belief in polyphyletic origins it will be clear that any simple serial sequence of the larger groups would inevitably be misleading. The general discussion of the facts, whether from the point of view of general morphology, of an evolutionary grouping of archegoniate plants, or of their relation to the establishment of a Land Flora, will be deferred till the concluding Chapters, when a wide observational field will be available for use.

PART I

CHAPTER I

THE ANTHOCEROTALES ¹

THIS group of Liverworts is widely spread, especially in tropical and warm temperate regions. It includes three well-known genera, viz., *Anthoceros*, *Dendroceros*, and *Notothylas*; the first and last inhabit temperate rather than tropical zones, and are ground-dwellers; but *Dendroceros* is confined to the tropics: it is of greater size, and is epiphytic on stems and leaves of larger plants. Together they form a natural series that shows a general relation to other Liverworts, but no close affinity to any particular group of them. They possess features both of gametophyte and of sporophyte which are peculiarly their own, and are of special value for comparison. Hence they are best treated apart—as the Anthocerotales.

THE GAMETOPHYTE

The gametophyte appears as a prone thallus with or without a midrib, and leafless. In the smaller types it develops from the parent spore as a centre, with more or less regular dichotomy, so as to form a rosette of strap-shaped branches attached by rhizoids to the soil (Fig. 3). In the larger genus, *Dendroceros*, there is a less freely branched thallus with a midrib projecting below, and lateral wings one layer of cells in thickness; these are much folded and lobed, so as to give an almost foliar character. In some forms of *Anthoceros* also the margins and surface of the thallus may grow out into irregularly crowded and fimbriated lobes (*A. arachnoides*, *fimbriatus*), to

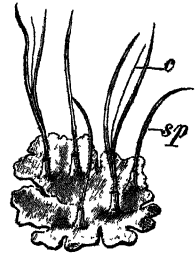


FIG. 3.
Anthoceros laevis. Thallus bearing sporogonia. *sp*, sporogonium; *c*, columella. Nat. size. (After Strasburger.)

¹ *Selected Literature on the Anthocerotales*: Hofmeister, *Vergl. Unters.*, Leipzig, 1851. *Higher Cryptogamia*, Ray Soc., 1862. Leitgeb, *Lebermoose*, 1874-1881, v. Schimper, "Chlorophyllkörper," *Pringsh. Jahrb.*, 1885, Bd. xvi. Scherrer, "Chromatophoren von *Anthoceros*," *Flora*, Bd. 10. Lang, "Apospory in *Anthoceros*," *Ann. of Bot.* xv., 1901, p. 503. Lang, "Notothylas," *Ann. of Bot.*, xxi., 1907, p. 201. Cavers, *New Phyt.*, Reprint, No. 4, 1911, where the literature up to date is fully quoted. Campbell, *Mosses and Ferns*, 1918, chap. iv., where literature is fully quoted. Campbell, "*Anth. fusiformis*," *Ann. of Bot.*, xxxviii, 1924, p. 473. Von Goebel, *Organographie*, iii. Aufl., ii. Teil, 1930, *passim*. Verdoorn, *Manual of Bryology*, 1932, *passim*. S. K. Paude, "*Notothylas leuieri*," *Current Science*, vol. i., March 1933, p. 272.

which Von Goebel ascribes a water-retaining function. Except for these, and rhizoids, the Anthocerotales have no appendages.¹

The deeply emarginate growing point is constructed as in the Marchantiaceae.² One four-sided pyramidal apical cell undergoes fission so as to produce segments right and left, adding thus to the expanse; other segments are cut off alternately above and below, providing for the fleshy thickness of the thallus (Fig. 4, A). The thallus itself consists of soft parenchyma;

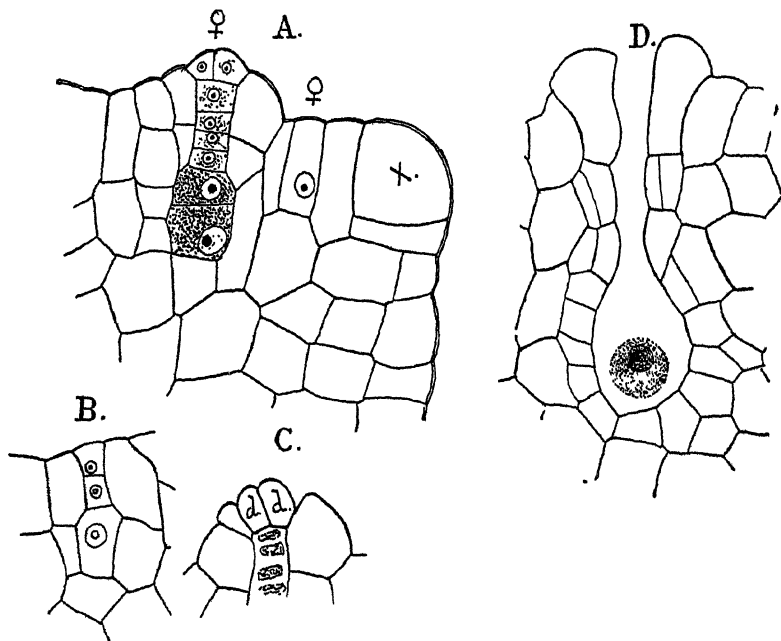


FIG. 4.

Anthoceros fussiformis. A, vertical section of the growing point showing archegonia (♀); B, young archegonium; C, upper part of a nearly ripe archegonium; d, d, the cover-cells; D, an open archegonium. $\times 600$. (After Campbell.)

each cell contains usually one large chloroplast, resembling those of certain green Algae. Sometimes more than one of them may be present, and each may enclose a pyrenoid. Thin-walled rhizoids grow out from the ventral surface. A peculiar structural feature, of occasional but not constant occurrence, is the presence of stoma-like clefts upon the lower surface of the thallus, which open into cavities filled with mucilage. Into these cavities filaments of *Nostoc* have been seen to find their way, and developing, establish those colonies which have long been known to inhabit the thallus; they appear as a natural invasion of a suitable habitat by a space-parasite.

¹ *Organographie*, iii. Aufl., ii. Teil, pp. 708, 771.

² Campbell, *Mosses and Ferns*, 1918, chap. iv.

Air-containing channels are absent from the thallus of the Anthocerotales, though present in the sporogonium. The only form of vegetative propagation in the group appears to depend upon a marginal formation of stalked storage tubers in certain species of *Anthoceros*; these germinate after a resting period to form new gametophytes. Sometimes, however, the tips of branches may persist from year to year without marked storage, and renew their growth when the conditions are favourable.

The sexual propagation is by antheridia and archegonia, both of which are sunk deeply in the fleshy thallus. The Anthocerotales seem never to form special sexual branches of the thallus, nor are there any protective developments for the gametangia. In this they may be held as primitive.

At most the fertile branches may sometimes be distinguished as relatively small appendages upon those of the normally sterile type. The sexual organs originate close to the apex, and usually from the upper segments of the initial cell. They thus appear upon the upper face of the thallus; but this is not constantly so. All three genera are monocious. Though Leitgeb found in abnormal cases that the antheridia may arise superficially they are normally endogenous, and are borne sometimes singly, some-

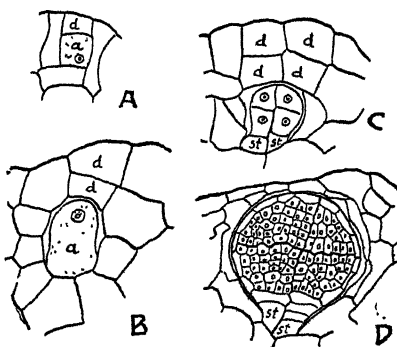


FIG. 5

Anthoceros Pearsoni. Development of the endogenous antheridium: *d*, covering cells; *st*, stalk-cells; *a*, young antheridium. (After Campbell, from Strasburger.)

times in groups. In either event each group can be traced to a single superficial cell, which lies close to the apex itself (Fig. 5). This cell undergoes periclinal fission; the outer portion divides again to form a two-layered wall (*d*), while the inner either develops at once into a single antheridium or, as in most species, it divides by crossed anticlinal walls to form two or four antheridial mother-cells. As the mother-cell rounds off preparatory to segmentation the cells surrounding it withdraw, forming a space filled with mucilage. Each mother-cell usually divides by intersecting longitudinal walls. Each of the four cells divides transversely; the basal portions go to form the stalk (*st*); each distal portion again divides transversely, giving an octant of cells from which the body of the antheridium is formed. Each of the eight cells then divides periclinally, the outer portions forming the antheridial wall, while the spermatocytes result from repeated intersection of the inner portions (Fig. 5). Secondary antheridia often arise later by budding from the base of the older ones, and their number may be variable. The sperms are discharged by separation of the apical cells of the antheridium, and they resemble those of other Hepaticae.

The archegonia appear later upon the same thallus, and in acropetal order, close to the growing point. Each dorsal segment of the initial cell of the thallus may give rise to one of them (Fig. 4, A). An outer cell cut off by its first periclinal wall is the mother-cell of an archegonium. Three vertical intersecting walls cut out from it a central triangular cell, as in other Hepaticae; here, however, the archegonium, consisting now of four cells, does not project, but is completely sunk in the tissue of the thallus (Fig. 4, A). The whole group of four cells then divides in the manner usual for Liverworts into two tiers: the three cells of the sunken neck divide again by vertical walls, so that six rows are formed, surrounding the axial cell. This divides first into two of nearly equal size, but the inner soon becomes more distended than the outer. By a periclinal division the latter forms externally the "cover-cell," and internally the "primary neck-canal-cell" (B, C). The cover-cell divides again by crossed anticlinals to form the distal rosette, while the neck-canal-cell forms a chain of four or more canal-cells. The inner cell resulting from the first periclinal division of the axial cell has meanwhile enlarged, and finally it gives rise to the ventral-canal-cell, and the ovum (A). At maturity the cover-cells are thrown off, leaving no trace, and the canal opens widely (D); it contains mucilage and the remains of the canal cells, while the ovum occupies the enlarged venter. It is thus seen that in essentials this segmentation is similar to that in the archegonia of other Hepatics. It follows from this description that both of the sexual organs of the Anthocerotales, though differing in certain details from other Hepaticae, are clearly of the Hepatic type; and this is so notwithstanding that they alone are deeply sunk in the fleshy thallus, and that the antheridia are even endogenous in origin. The impression conveyed is that this biological protection is probably a special and secondary condition rather than a primitive state.

THE SPOROPHYTE

The sporophyte of the Anthocerotales is peculiar among those of the Bryophyta in certain essential features. Recent discoveries have brought it into closer comparison than before with the sporophyte in certain vascular plants. It therefore claims special attention. In form it is like an elongated spindle with an enlarged base, or foot, by which it is attached to the gametophyte; a sheath or involucre of gametophytic tissue envelops the weak intercalary zone below, thereby giving mechanical support. While young the sporogonium is terete and green up to the tip; but as it ripens it ruptures longitudinally by slits which extend progressively downwards. Two valves are thus separated which diverge, while a thread-like columella projects between them (Fig. 3). Freedom is thus given to the spores, and to the elaters that are usually associated with them. The surface of the sporogonium

while young is dotted with stomata which lead to a system of intercellular spaces ventilating the green photosynthetic tissue ; the capsule is thus at least partially self-supporting. A peculiar feature is the continued intercalary growth, which is located in a zone above the enlarged base. Provision is thus made for increase in length of the spore-producing capsule from below ; and for a continued succession of spores. In this the Anthocerotales

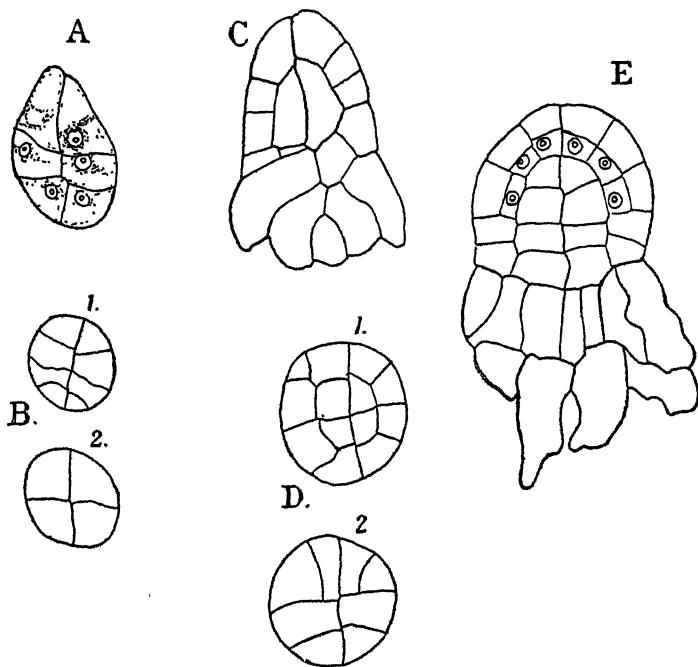


FIG. 6.

Anthoceros Pearsoni. Development of the embryo. $\times 300$. A, C, E, median longitudinal sections. B and D, successive cross-sections of embryos of about the age of A and C respectively. In E the archesporium is differentiated. (After Campbell.)

The embryos are orientated so that the apex points to the neck of the archegonium. The embryogeny is thus exoscopic.

stand alone among the Bryophyta. A dense tuft of young sporogonia thus constructed looks while young like fine grass-leaves ; but after dehiscence the valves turn grey or brown ; nevertheless, intercalary growth may still be continued below, long after dehiscence has begun at the distal end. The capsules of the Anthocerotales are all built on the same plan. However different they may appear to be from those of other Bryophytes there are essential features of similarity, particularly with the Jungermanniaceae. These will intensify the interest in the study of their development.

This has been carefully studied in *Anthoceros* by Campbell.¹ The early segmentations result in three tiers composed of four cells each (Fig. 6, A) : of

¹ *Mosses and Ferns*, 1918, p. 136.

these the lowest is derived from the hypobasal half of the zygote, and it forms the main part, if not indeed the whole of the foot. The highest tier gives rise to the primary capsule, while from the intermediate zone derived from the second tier the meristematic part of the older sporogonium

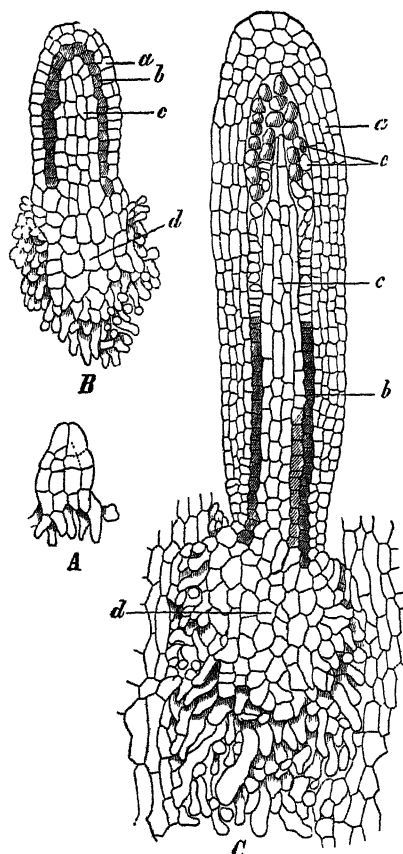


FIG. 7.

Sporogonia of *Dendroceros*. A, very young sporogonium of *D. cichoriaceus*. B, slightly older of *D. crispatus*. C, still older of *D. crispatus*. a = capsular wall; b = archesporium; c = columella; d = foot (haustorium) with its tubular absorbing cells; e = spore-mother-cells. (After Leitgeb, from Engler-Prantl, *Natürl. Pflanzenfam.*)

in the Bryophytes generally the embryology is exoscopic, the apex being directed towards the archegonial neck.

Meanwhile the foot becomes specialised as a haustorium; by forming tubular outgrowths which penetrate the tissues of the gametophyte the absorptive surface is increased and its range extended (Fig. 6, c, e). This is particularly well seen in the large sporogonium of *Dendroceros*,

is formed (Fig. 6, e). The highest tier of four cells segments further to form a central group of four, and a peripheral series (Fig. 6, c, d): from the former the sterile columella originates, although in all other Liverworts the corresponding cells give rise to the archesporium. This, however, is primarily formed in *Anthoceros* from the inner cells resulting from periclinal division of the peripheral cells of the highest tier, and its form is that of a dome completely covering the rounded apex of the columella. The latter thus initiated in *Anthoceros* develops entirely as sterile tissue. The layer of cells immediately outside it is recognised as the archesporium by their denser protoplasm (Fig. 6, e). Subsequently an intercalary activity begins in the middle zone; it adds by basal increments respectively to the columella, the archesporial layer, and to the capsular wall. Such intercalary development was probably of secondary origin: if this were so the primary condition of the sporogonium of *Anthoceros* would be a more satisfactory basis for comparison with other Bryophytes than the state adopted later in the ontogeny. As

which is constructed on the same plan as that of *Anthoceros* (Fig. 7). On the other hand, the capsular wall above assumes an active photosynthetic function. Each of the cells composing it contains as a rule two large chloroplasts, similar to those of the gametophyte. In *Anthoceros* a superficial epidermis is composed of elongated narrow cells much like those of the elongated leaves of Monocotyledons. But certain cells cease to elongate, maintaining an oval form. Each of these divides longitudinally by a septum that splits, forming a pore surrounded by two guard-cells, as in a normal stoma. The pores open into well-developed air chambers, so that a typically ventilated photosynthetic system results (Fig. 8). But this structure is not constant in the family. No stomata are recorded in *Dendroceros* or in *Notothylas*, the largest and the smallest types.

The interest in the sporogonium naturally centres in the products of the archesporium, and its relation to the sterile tissues that bound it within and without. The dome-like form, as it passes without interruption over the tip of the columella, is unusual in Liverworts; but it finds its correlative in *Sphagnum* (see p. 64). As the intercalary growth of the sporogonium proceeds the distal region is carried up on the lengthening spindle. The youngest stages of development of the archesporium may be seen at the base (Fig. 7): all stages of tetrad-development may be followed upwards, till the fully matured spores are set free by the distal rupture. The stages are thus easily followed in a single individual, and advantage was taken of this by Von Mohl in his early description of the division of spore-mother-cells. At the base the archesporium appears as a single layer of cells, which separate and differentiate to give (i) oval swollen cells with nucleus, chloroplast, and granular cytoplasm; these are the spore-mother-cells; and (ii) more slender cells which are in fact sister-cells with the latter, and undergo division, giving rise to the pluricellular elaters. They are disposed together with some degree of regularity in alternating groups. The elaters of *Anthoceros* have usually smooth walls and have a nutritive function; but in *Dendroceros* they are spirally thickened and are effective in spore-distribution, as is usual in the Hepaticae. The spore-mother-cells contain each a relatively small nucleus and a large chloroplast. In the course of tetrad-division both nucleus and chloroplast undergo successive divisions, so that each spore contains a representative of both. When mature they are thick-walled.

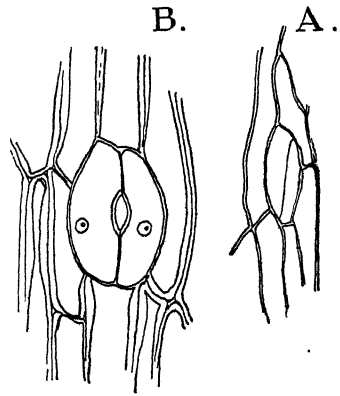


FIG. 8.

Stomata from sporogonium of *Anthoceros Pearsoni*. $\times 250$. A, young; B, fully developed. (After Campbell.)

The chromatophores of *Anthoceros* have been examined by A. Scherrer (*Flora*, Bd. 107, Heft i., pp. 1-56). He finds that they remain as morphological individuals throughout the development of the gametophyte and sporophyte. Their multiplication is exclusively by division. The egg-cell and the spore each contain continuously one well-developed chromatophore; but the male gametes have none. A doubling of the number of chromatophores in *Anthoceros* is therefore not a direct consequence of syngamy. A study of the tissues of the sporophyte by Schimper has shown that "in the cells of the sporogonium of *Anthoceros* the first indication of the fission of the hitherto single chromatophore takes place: most of its cells possess two, those of the epidermis several chromatophores" (*Pringsh. Jahrb.*, 1885, Bd. xvi., p. 1). This appears to be a special example of that general progression already indicated by De Bary, from a single chromatophore in each cell, which is characteristic of the lower types of plants, to many, which is characteristic of the higher (*De Bary, Bot. Zeit.*, 1881, p. 1). The special interest of *Anthoceros* in this relation is that in its tissues, whether of gametophyte or of sporophyte, but especially of the latter, the number of chloroplasts is highly variable. It can hardly be doubted that there is an underlying size-relation in this, though exact measurements are still wanting (Bower, *Size and Form*, 1930, p. 218). Pyrenoids are not constantly present: the chromatophores of *A. Husnoti* and *punctatus*, the two species examined by Scherrer, may perhaps be held as intermediate between those with and those without pyrenoids, such as are seen in other species of *Anthoceros*.

It might be difficult, in the absence of intermediate forms, to bring the peculiar sporogonium of *Anthoceros* into relation with those of other Liverworts. But within the Anthocerotales there is the genus *Notothylas*, which bears sporogonia of small size and limited in intercalary growth. In these small sporogonia, though a sterile columella is often present, sometimes its place is taken by fertile tissue. The details of this were long ago described by Leitgeb (*Lebermoose*, v., p. 39); but later his conclusions were called in question. The observations of Lang go far to explain the discrepancies; they show that as regards potential fertility Leitgeb was substantially correct (Lang, *Ann. of Bot.*, vol. xxi, p. 201). It appears that the embryonic structure of the sporogonium of *Notothylas* is essentially like that of *Anthoceros*. In those cases where the columella is present in the mature state the spore-mother-cells originate only from the amphithecial archesporium. But in others where a definite columella is not present in the mature state, any cell of the tract laid down structurally as columella may develop as a spore-mother-cell. Many do so, and thus, as Leitgeb described, the place of the sterile columella may be taken by a spongy mass of sterile tissue, in the meshes of which spores are included. In addition to this, however, fertile cells and elaters are also produced from an archesporium, which lies, as in *Anthoceros*, outside the columella (Figs. 9 A-F). These facts throw considerable light upon the relation of the columella-less to the columelloid forms: they increase the justification for considering the central group of cells,

which in all other Anthocerotaceae is wholly devoted to the formation of a sterile columella, as an original sporogenous tissue, and the amphithecial archesporium as of secondary origin. The duty of producing spores would seem to have been transferred from the central to a more superficial set of cells. It is thus possible to bring the apparently divergent sporogonium of

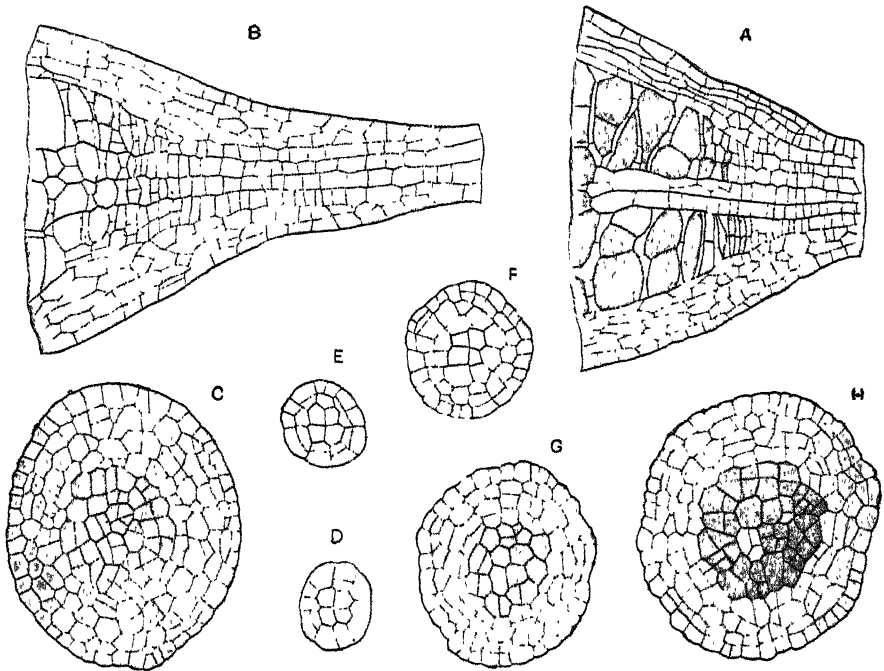


FIG. 9.

Notothylas Breutelii. A, longitudinal section of the basal region of an almost mature capsule, showing a short sterile columella derived from the endothecium. $\times 130$. B, a similar section, but without sterile columella. In the upper part the wall of the capsule can be distinguished from the sporogenous tissue, the cells of which are differentiated into spore-mother-cells (shaded), and elaters. Traced downwards, the central portion of the sporogenous tissue is continuous with the endothecium, while the peripheral portion comes from a layer of cells which have a common origin with the wall. $\times 170$. C, transverse section of a sporogonium like B, at the base of the fertile region; the uniform sporogenous tissue (shaded) can be seen to be composed of four central groups of cells (endothecium) and a surrounding layer derived from the amphithecium. $\times 170$. D, E, F, G, H, successive transverse sections of a sporogonium, in which one of the four rows of cells of the endothecium is forming a sterile columella, left clear in G and H. $\times 170$. (After Lang.)

the Anthocerotales into relation to that of the Jungermanniales where the archesporium is wholly endothecial. The causes of the change of the products of the endothecium from the fertile to the sterile condition must be looked for in influences acting on the primary meristematic tissue of the embryo, or on the intercalary zone of secondary meristem. Dr. Lang holds that the idea of a grouping of elaters in a central position to form the columella is not in this case in accordance with the facts (*l.c.*, p. 208). These

suggest rather the influence of nutritive factors acting on the young embryo while still enclosed in the tissue of the gametophyte.

In contrast to these small sporogonia of *Notothylas*, with their evanescent columella, may be placed those large sporogonia of *Anthoceros fusiformis* described by Campbell (*Ann. of Bot.*, xxxviii., 1924, p. 473). In normal specimens the columella consists of about sixteen prismatic cells, arranged in an almost perfect square, as seen in transverse section near the base. It is surrounded by the archesporium, outside of which are about three layers of photosynthetic cells, the outermost forming a distinct epidermis. Higher up a large lacuna replaces the archesporium, and surrounds the columella,

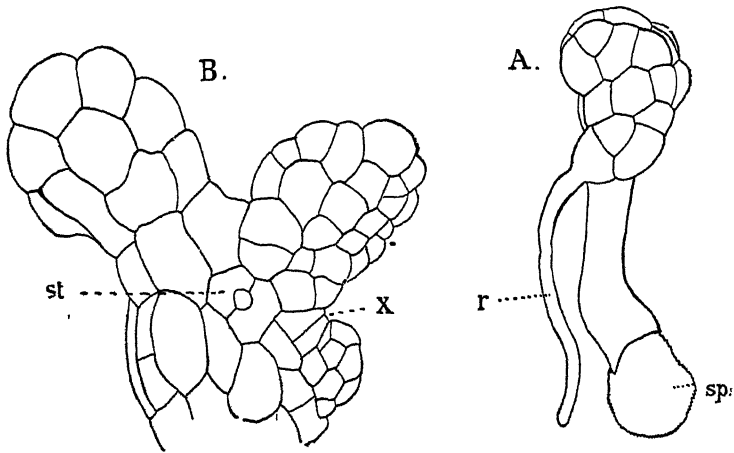


FIG. 10.

Anthoceros fusiformis. A, germinating spore (sp), with young plant showing the first rhizoid (r). B, upper part of an older plant with the first mucilage-cleft (st); x, the growing point. $\times 215$. (After Campbell.)

which finally dries up and produces a bundle of isolated fibres. But in certain large specimens collected in California by Peirce, some six inches in length, which had been growing for nine months or more, the structure of the columella was more coherent. The plants were more bulky; their basal region was still green for about two inches, with hypertrophy of the lower part, and distally only a short fertile tract. At the base the columella appeared normal; but higher up it was much larger, and it remained connected by sterile cells of the archesporium with the external green tissue. Campbell describes how here "the columella is nearly twice the diameter of that of the normal sporophyte, and in longitudinal section it appears as a stout strand of elongated cells highly suggestive of a simple vascular bundle." With this there appeared a corresponding increase of the amount of green tissue to more than twice that of the normal form. There was also evidence that the surface of the foot was exposed by disorganisation of the gameto-

phyte, and probably it absorbed water from the soil. Thus these large sporophytes appeared to him to have "reached a condition comparable to that of the young Pteridophyte after it has established its first root." No one can deny the interest of these observations as suggesting a possible step in evolution. The question will be whether it can be inferred from them that any Pteridophytic sporophyte did actually acquire its independence in this way.

After the spores are shed a resting period follows: on germination the wall of the spore splits along the diverging quadrant ridges, and a germinal tube of variable length protrudes which divides at first by transverse septa; then by intersecting walls the terminal cell forms four quadrant cells after the manner of the Hepaticae. Segmentations sometimes suggestive of a single apical cell follow, and finally a growing point is established, while marginal lobes appear irregularly, giving the whole thallus a crimped appearance. Campbell compares that of *A. fusiformis* with the prothallus of *Equisetum*. Rhizoids, mucilage-slits, and Nostoc-infection then follow, and so the thallus passes to the adult state (Fig. 10).

It is worthy of remark that the Anthocerotales appear to be singularly free from fungal infection, and of mycorrhizic symbiosis. In this they resemble the Mosses rather than the Liverworts.

COMPARISON OF THE ANTHOCEROTALES

The Anthocerotales are a very natural and distinctive family of plants. This is borne out on the one hand by the relative uniformity of the features of the gametophyte and sexual organs, and on the other by those of the sporophyte with its basipetal spore-production. The family comprises no single type which suggests a linkage with any one particular series of the Liverworts. Nevertheless it cannot be doubted that their relation to these plants is closer than to any other. This appears to follow especially from the comparison of their sexual organs. Notwithstanding the sunken position of these, and the fact that there are certain differences in the details of their segmentation from those of most Liverworts, still in essential construction there is similarity of both antheridia and archegonia to some generalised type which would include all Liverworts. This comparison is borne out again by the initial characters of their sporogonia, though these also possess peculiar features in the adult state. The conclusion from such considerations will be that the place of the Anthocerotales is with the Liverworts, but not closely with any section of them. On the other hand, as Von Goebel points out (*Organographie*, ii., p. 687), features of the antheridium, and particularly of the sporogonium, point towards the Sphagnaceae and Andreaeaceae, and so onwards to other Mosses (Chapter IV). Lastly, there are features of the sporophyte that suggest some distant comparison with the Psilophytales, which rank among the most primitive of known Vascular Plants (Chapter VII). Thus the Anthocerotales, though properly

placed as relatively primitive Bryophytes, appear as a synthetic type. That is the reason why they have been taken first into discussion here.

No near alliance can be claimed for them with any of the Green Algae : still less with the Red or the Brown. It is true that some common features do exist : such as the similarity of the chloroplasts and their pyrenoids to those of certain of the Chlorophyceae, or the outline and branching of the gametophyte. But such points are of a general nature, and they are not so many or so consistent as to suggest any near affinity. It thus appears that the Anthocerotales are an isolated group of very primitive Land Plants.

Instead of driving comparisons of detail to an extreme limit, with a view to tracing affinities for plants thus isolated, it would seem more fruitful to enquire how the characteristic features of the Anthocerotales have qualified them to secure a footing as land-dwelling plants ; and on the other hand to consider their shortcomings as explaining their lowly state : using them, in fact, as a means of introducing certain aspects from which other archegoniate plants may be studied and compared. Their life-history is, like that of all plants possessing sexuality, based upon the nuclear cycle with its critical points of syngamy and reduction. The two somatic phases that intervene give the characteristic alternation. These plants suffer from the disability common to all Archegoniatae of being dependent upon external liquid water for their fertilisation. As a set-off against this their survival on land and their spread over its surface would be more readily secured in the first instance by accommodation of the vegetative system of both phases to sub-aerial life. These may be held as separate but inter-dependent developmental propositions. Being parts of the same individual life-cycle the "temperament" of both will be essentially the same, though the evolutionary history, the time of origin, and the biological end of the one may have been different from that of the other. Thus, from the developmental point of view, the two vegetative phases may be studied along parallel lines. The solution of the evolutionary problem for both, in terms of form and function, may well in the first instance have followed courses not wholly unlike. At the same time the fact that the one is haploid and the other diploid, with all that this connotes, is to be fully borne in mind. We know from experience that in both the kingdoms of living things the higher development has been attained by the diploid phase.

The ordinary conditions of life underlie the problem of form and structure for any evolving type of land-plants. The most important of them are exposure to air as a rule not saturated by water vapour, access to water-supply from the soil or from some other sources liable to be intermittent, and suitable conditions of temperature and light ; while the effect of gravity acts as a directive or moulding influence, and creates a demand for mechanical stability under subaerial conditions. Over and above such demands, which are all variable in their incidence, there is also the ever-present and unavoid-

able factor of size of the organism itself, or of its parts; and the insistence of this increases with the dimensions. The effect of the size-factor works out primarily in relation to mechanical stability, the demands for which are for the most part met by adjustments of internal structure, though partly also by modifications of external form; but, secondarily, in the requirement for maintenance of a due proportion of the several surfaces of transit (presentation surfaces) to the bulk which they enclose as the size increases. The result appears as elaboration of form, whether of external surfaces or of the boundaries of internal tissue-tracts and of the cells that compose them. In fact, increasing size acts as a morphoplastic factor, with the general result that the larger the organism or its parts the more elaborate the form and internal structure will need to be (Bower, *Size and Form in Plants*, 1930). Such is the framework of circumstance within which the amphibian plant lives to-day, and it may be presumed that it was under like conditions that the evolution proceeded.

We may now consider the alternating phases of the Anthocerotales severally from the point of view thus sketched, marking on the one hand their features of achievement, and on the other their limitations and disabilities as compared with plants higher or it may be lower in the scale. This analysis applied to a definite and isolated family may form a useful preparation for comparisons of wider scope.

The germination of the spore of *Anihoceros* gives the most convenient starting point. The germinal tube that emerges from the ruptured wall is cylindrical, and of variable length. The differences are probably dependent upon external conditions, particularly on the intensity of the incident light. Enlargement appears at the distal end accompanied by cell-cleavages; these vary in position and in number: where the diameter remains relatively and uniformly small they are transverse, but, where the size increases distally, the later walls of cleavage intersect, forming a solid, obconical body. A growing point is soon established (α , Fig. 10). Sooner or later the thallus becomes strap-shaped, and it settles down to the average width and thickness for the species. But it is not internally ventilated; consequently with increase in the size of the thallus the proportion of the external presentation-surface to bulk falls, without that remedy of internal ventilation which is usual in subaerial plants. This difficulty is in a measure met by the dorsiventrally flattened form, which gives a higher proportion of surface than a conical or cylindrical form would do. The further development is by apical growth and branching, rather than by increasing mass of the thallus. Marginal and superficial flaps or lobes tend also by elaboration of form to maintain the proportion of surface to bulk, particularly in the large thallus of *Dendroceros*. The result is that the gametophyte of the family never attains any great size, while the largest species tend to be the most elaborate in outline.

In this connection the mucilage-clefts present a special interest. A near structural similarity between these clefts and normal stomata has been traced by Von Goebel, and the comparison has been extended by him to the

air-pores of the Marchantiaceae (*l.c.*, p. 674). On the other hand, normal stomata are present on the sporogonium of some of the Anthocerotales. The bearing of these facts will be discussed at the close of this Chapter.

The deeply sunk sexual organs of the family contrast sharply in position with those of other Bryophytes. But their development and structure are such as to leave no doubt of their essential correspondence with these, while the occasional presence of antheridia that are not endogenous tends to confirm this view. The facts may be accepted as related to the fleshy habit of the thallus; together they appear as a provision against the risk from drought. The whole structure of the flattened gametophyte of the Anthocerotales suggests a somewhat clumsy compromise of structure to meet two conflicting needs: on the one hand giving security against exposure to surface-evaporation; and on the other providing, in the absence of internal ventilation, against a deficiency of presentation-surface so necessary for gaseous interchange. Meanwhile the plagiotropic habit gives a high probability of access downwards to liquid water for fertilisation. The result is that the gametophyte is efficient for life in a damp habitat, though it remains as a relatively small, creeping thallus.

The sporophyte of the Anthocerotales suffers also from certain disabilities, but they are complementary to rather than identical with those of the gametophyte, over which it possesses certain advantages. It is dependent throughout its life upon the gametophyte for its water-supply and salts, and especially at first for its organic food as well, while its central columella is believed to play a part in conduction. The form is approximately cylindrical, which gives a relatively small proportion of surface to bulk. But against this is to be set the presence in certain types of functional stomata, which lead to an effective system of intercellular spaces, thus increasing the presentation-surface for gaseous interchange. On the other hand, localised apical growth and branching are both absent. But against this again is to be set the intercalary growth at the base of the fertile region, which not only provides a progressively increasing photosynthetic system, but also a continuous succession of spores set free by the basipetal rupture of the sporogonium; moreover, the drain of spore-production is spread over a prolonged period. It thus appears that, notwithstanding certain features of advance, the sporogonium is of relatively low organisation; in particular it never departs from the simple spindle-form. But this rudimentary state does not rest upon the same details as those which tend to limit the development of the thallus. Moreover, it is to be remembered that the biological end is in either case different: the development of the gametophyte leads up to syngamy through the medium of liquid water, that of the sporophyte to production and dissemination of the spores through dry air. Accordingly the apex of the one is depressed, and of the other erect.

Such results from the comparison of the two alternating phases as are seen in these primitive land plants raise the question of their relation one to another in point of evolutionary origin; and the problem naturally extends itself to other archegoniate plants. The whole subject of alternation will be taken up in Chapter XXIV. But meanwhile the more immediate question relates to the evidence which the Anthocerotales themselves afford. Normally

the life history fits on to a regularly recurrent nuclear cycle, with syngamy and reduction as its critical points.¹ While the haplophase is independent throughout, the diplophase is physiologically dependent upon it for nutrition, at first wholly and later partially. This may appear as primary evidence of an initial dependence of the latter throughout descent; but the alternative cannot be excluded, that the dependence may have been acquired. On this point the facts for this family alone afford no definite proof. It is possible that an originally free embryo may have been retained secondarily, in accordance with the advantage of being nursed during its initial stages; this Prof. W. H. Lang has suggested for archegoniates generally (*Linn. Journ.*, 1909; *New Phyt.*, vol. viii., p. 104).

An important general feature of the Anthocerotales is that, notwithstanding the contrasts which the two alternating phases present, in apical growth and in internal ventilation, there is a higher degree of similarity in their general structure than in any other Bryophytes. Both are mostly composed of photosynthetic cells, containing one or more chloroplasts of large size, which multiply by fission. It is significant that their number is habitually larger in the sporophyte; and this phase is characterised in the vascular Archegoniatae by a higher degree of organisation in other respects also. The Anthocerotales show in this detail of chloroplast-number a scale of variation towards the state habitual in the higher plants, viz., that with numerous small chloroplasts. On the other hand, the large chloroplasts that occur singly, and are the rule in the gametophyte, are closely similar to those of some green Algae. The variability seen in the Anthocerotales bridges this difference between certain Algae and land-vegetation.

A striking feature for comparison in the two phases is the existence of pores of stomatal character on both haplophase and diplophase. The similarity of their structure is such that Von Goebel recognised their homology. Structurally, as seen in surface view, the similarity is impressive (Fig. 11). While they are distributed all round the terete sporogonium they may appear not only on the lower but also on the upper side of the thallus. It is true that while those of the diplophase lead to an internal ventilating system those of the haplophase lead only to passages filled with mucilage. But it is possible that the mucilage-clefts of the latter also were originally open air-ways, leading like normal stomata into an internal ventilating system, which originally permeated the gametophyte as it now does the sporophyte, and that the choking of the system was related to the assumption of a moist habitat, and of a prone in place of an upstanding habit. *A picture would thus be suggested of the original haplophase of the Anthocerotales as a fully equipped photosynthetic structure, probably terete like the present diplophase.* Von Goebel regards the sporophyte as having proved itself more conservative than the gametophyte in its vegetative structure (*l.c.*, p. 678). If this were so the alternating phases would have originally resembled one another to a degree that finds its parallel

¹ In 1901 (*Ann. of Bot.*, xv., p. 503) Lang described how aposporous growths had been obtained by cultivation of pieces of the sporogonium of *Anthoceros laevis* on damp sand. They commonly arose from sub-epidermal cells, but other layers of the sporogonial wall may take part exclusive of the sporogenous layer. Here as elsewhere it is the least specialised cells that are the source.

in certain Algae, for instance in *Dictyota*, and in some degree in the Archegoniatae: for instance in *Lycopodium* (Fig. 200). Nor does this seem biologically improbable, since the subaerial conditions for primitive land-plants would have been the same for both at first, as they are also in the submerged diplobiontic Algae.

Such similarity between the alternating phases of any diplobiontic organism does not by any means imply strict community of their origin. If each had actually arisen as a distinct somatic development imposed upon the usual nuclear cycle under uniform conditions, it would appear natural that their structure should be alike, being phases of the same organism. But they

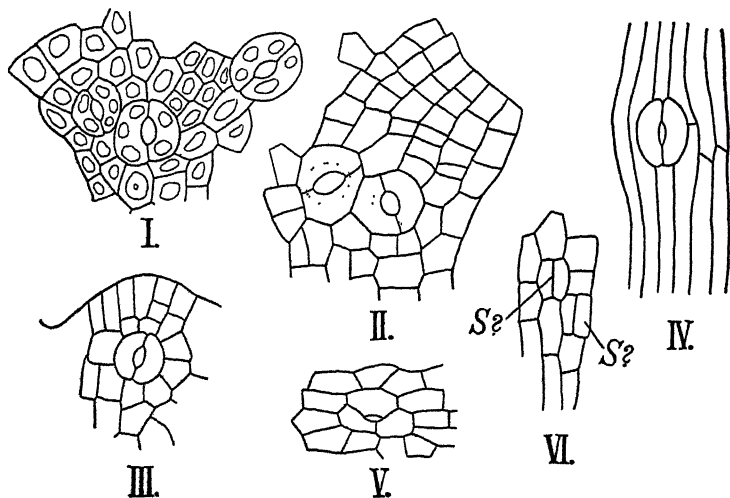


FIG. 11.

I. *Dendroceros* sp. Part of lower surface of thallus, before branching, with three stomata, whose guard-cells have more than one chloroplast, though one only is in the neighbouring cells. II., part of lower surface near to the growing point in a species of *Anthoceros* from Rio. III., the same from a New Zealand species of *Anthoceros*. IV., stoma from a sporogonium of *Anthoceros*. V., a stoma from the thallus with a divided guard-cell. VI., piece of epidermis of a sporogonium of *Dendroceros crispus*. (After Von Goebel.)

would not be strictly homogenetic, the one being pre-sexual and haploid, the other post-sexual and diploid. As a conclusion based on a wider comparison than that from any single family Von Goebel has pointed out that, "The gametophyte and the sporophyte resemble one another most in those groups of the Bryophyta which are most clearly recognised by their cell-structure as primitive. Where in other Bryophytes differences rule, this depends upon change whether in gametophyte or in sporophyte; such changes may be deduced from comparative study of the living forms" (*l.c.*, p. 681).

This similarity between the alternating phases of the Anthocerotales may be held as according with other primitive characters which they possess. By comparing them with other Archegoniate types from the point of view sketched in the preceding paragraphs, various probable lines of biological

progress are suggested, whether of elaboration or of simplification. These are found to involve :—

(i) Increasing divergence in character of the two generations, in accordance with their respective ends of syngamy and spore-production.

(ii) Localisation of growth, whether apical or intercalary, and finally the establishment of a scheme of construction that is theoretically unlimited.

(iii) Adjustment of form in accordance with the increase in size of either of them, and with their functions and external conditions ; in particular, the adoption of a branched habit in the sporophyte.

(iv) Elaboration of internal structure, particularly in respect of conduction and internal ventilation.

(v) Adjustment of the nutritive system to the requirements of self-nutrition, or of physiological dependence.

(vi) Adjustments so as to secure the efficiency and protection of the sexual organs.

(vii) Elaboration of the system for spore-production and dissemination.

All these lines of specialisation, which are suggested or lightly indicated by the Anthocerotales will claim attention ; but particularly the last. The Archegoniatae include the most successful types of homosporous land-plants : in them the numerical output of spores is a more direct factor of success than in the higher forms where sexual propagation follows those more precise lines which are associated with heterospory and a seed Habit. The production of large numbers of spores depends upon nutrition : hence the nutritive system and the spore-producing members must necessarily co-operate, and a suitable balance must be adjusted between them. In this *sterilisation* of potentially fertile cells, of which the Anthocerotales offer instances, has taken an important part.

As a primitive and imperfectly specialised group of the Bryophyta the Anthocerotales take a place of high significance in the comparative morphology of the simpler Archegoniatae. Their sporogonia have features in common with those of the Sphagnales and Andreaeales, and thus provide a link between the Liverworts and the Mosses. But it is not only among the Bryophytes, with which they have habitually been ranked, that such comparisons will lie. Their sporogonial features point also towards those of the simplest of the Psilophytales. *Thus the Anthocerotales appear as a suggestively synthetic Archegoniate Type.*

CHAPTER II

THE MARCHANTIALES¹

EVER since the publication of Mirbel's monograph on *Marchantia polymorpha*, which he presented to the French Institute in 1835, the name-genus of this order of Liverworts has been well known as regards its general features. It comprises relatively large plants widely distributed, and of complicated structure. Since the common native species lends itself readily to demonstration it has been held as a type of the order. But associated with it are other genera of plants, smaller and more simply constructed, though sharing most of the leading characteristics of *Marchantia*. These may be laid out in a comparative series, till finally we see in *Riccia* a type which in certain features is the simplest of all Liverworts. The coherence of the genera included in the order is indicated not only by the uniformity of their sexual organs, but also by the persistently thalloid nature of the dorsiventral haplophase which bears them. More particularly, however, it appears in the peculiar means by which ventilation is secured in the thallus, itself as a rule fleshy in its texture. It bears minute ventral lamellae and rhizoids on its lower surface. The diplophase, or sporogonium, differs markedly in structure from the haplophase in being of simple form, without any appendages, and entirely dependent upon it for its nourishment. It is relatively small and destitute of photosynthetic tissue. In this it contrasts sharply with what has been seen in the Anthocerotales. It will be a question for later discussion whether the series of the Marchantiales is one of advance or of reduction from the evolutionary point of view. In the first instance the description will be based upon the genus *Marchantia* as being the best-known example, but without prejudging this question.

THE GAMETOPHYTE

The haplophase—or gametophyte—is plagiotropic and broadly thalloid, with a more or less marked midrib; it is without lateral appendages of

¹ *Selected Literature on Marchantiales*: Mirbel, "Marchantia," *Mém. de l'Acad. des Sci. de France*, vol. xiii., 1835. Hofmeister, *Vergl. Unters.*, 1851. *Higher Cryptogamia*, Ray. Soc., 1862. Leitgeb, *Lebermoose*, 1874-78. Cavers, *Ann. of Bot.*, xviii., 1903, p. 87. Cavers, *New Phyt.*, Reprint No. 4, 1911, chap. ii., where the literature is fully quoted. Campbell, *Mosses and Ferns*, 3rd edn., chap. ii., 1918, where the literature is fully quoted. Von Goebel, *Organographie*, iii. Aufl., Teil ii., 1930; *passim*. Orth, *Flora*, Bd. 124, 1929, where the literature on internal ventilation is cited. Verdoorn, *Manual of Bryology*, 1932, *passim*.

foliar nature, though ventral lamellae cover the apex, and persist on its lower surfaces. It branches dichotomously, and the rhizoids which attach it to the soil are of two distinct types. The first to be formed on germination are smooth-walled; they are wide and stand out from the thallus. Those of the other type are narrower, and appressed to the surface of the thallus, forming a strand or skein along its median line, which is continued up the channels of the fertile branches; they are characterised by pegged processes which project inwards from the wall, and they contain no protoplasm when mature. The exact function of these two types in water-conduction is still an open question (Goebel, *l.c.*, p. 742). Associated with the rhizoids on the lower surface are the membranous scales already mentioned: they are arranged in one to three rows on either side of the midrib, and appear to be similar in origin to the ventral scales of the thalloid Jungermanniales; they are referable in morphological origin to those mucilage-hairs that

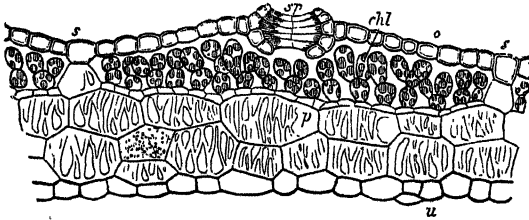


FIG. 12.

Transverse section through the thallus of *Marchantia*. *sp.* air-pore; *chl*, photosynthetic filaments. (After Haberlandt.)

protect the apex in many Liverworts, though here expanded into membranous flaps. An analogy may be pointed with the dermal hairs and scales found on the sporophyte of Ferns: in either case intermediate forms lead from the simpler hair to the flattened scale.

The deep-green upper surface of the thallus is marked by the well-known lozenge-shaped areas, each with a central air-pore, or "stoma"; sections show the elaborate ventilation of the chamber below each area, with its photosynthetic papillae within (Fig. 12). Each chamber is separated from its neighbours by partitions extending from the single-layered roof to the floor of colourless parenchyma, which contains occasional oil-cells. The structural analogy with the photosynthetic system of leaves is obvious: when grown in sunlight the green filaments may even take the form of palisade-tissue (Stahl). The critical points in this comparison will be the structure of the air-pore, and the origin of the air-chamber and its contents. The air-pores of *Marchantia* and *Preissia* are large and complicated. They appear as barrel-shaped structures, built up from some four tiers of cells which enclose a wide passage (Fig. 13). The lowermost tier projects more than the others into the passage, but it does not completely close it: a

channel like a four-rayed star remains open. In other allied genera the structure of the pore is simpler; for instance, in *Fegatella* or in *Targionia* there is no barrel-like structure surrounding the open pore (Fig. 14). Obser-

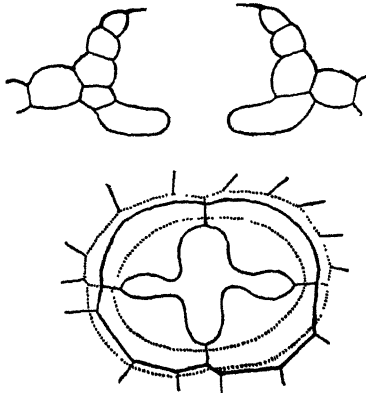


FIG. 13.

Air-pore of *Marchantia polymorpha*. Above, as seen in vertical section; below, as seen from underneath in order to show the papillose cells of the lowermost tier. (After Haberlandt.)

variations on the behaviour of the more complex types suggest some degree of closure of the pore on reduction of turgor of the cells, but the control cannot in any of these Liverworts be as efficient as it is in the stomata of Vascular Plants, notwithstanding their elaborate structure.

It is in certain of the larger thalloid forms that the highest elaboration of internal structure is found. *Marchantia* and *Preissia*, with their air-pores and ventilating chambers, appear as the culminating point. There is some variety in the form of the chambers in the different genera. In *Marchantia* and *Preissia* they are simple, and distinct from one another; but in *Wies-*

nerella the chambers, individually small, may be connected with other cavities in the thallus, forming irregularly branched chambers. Further, while in such genera as *Lunularia*, *Marchantia* and *Preissia* the cavities are occupied by secondary upgrowths which form the photosynthetic filaments, in others it is the cells adjoining the cavities that contain the chlorophyll, and

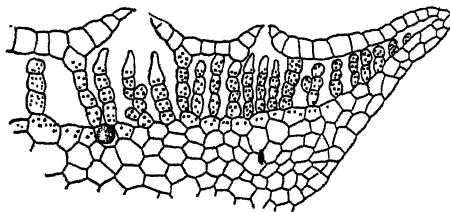


FIG. 14.

Vertical section through part of the thallus of *Targionia*, showing the air-cavities opening by simple pores on the upper surface, and containing filaments of chlorophyll-cells. $\times 75$.

carry on photosynthesis. This appears to be the condition in *Plagiochasma*, with its complex chambers that originate by splitting of cell-walls and extend deeply into the fleshy thallus (Fig. 15); also in *Riccia*, where the much simpler vertical slits arise in the same way. Following the opinion of Leitgeb it had been generally held that the cavities arise by surface-involution; but latterly evidence has been accumulated which shows that though this may have contributed to the result, a splitting of cell-walls, either from

without or even initiated within the tissue of the thallus, has been an active source of the chambered structure ; thus its origin is not altogether unlike that of the intercellular system in leaves of Land Plants.

The latest investigations on the subject have shown that in *Marchantia* and *Preissia* the chambers arise below the later formed skin as intercellular spaces. The pores are closed at first, and the canal results from splitting of anticlinal walls. In other Marchantiales that have been examined the chambers originate as depressions of the surface, but even these are formed not by upgrowth of cells but by a splitting of their walls that progresses gradually inwards. The result is either a simple widened chamber, or in case other splits appear in the thallus, a complex chamber, as in the instructive instance of *Plagiochasma* (Fig. 15). The difference is essentially one of

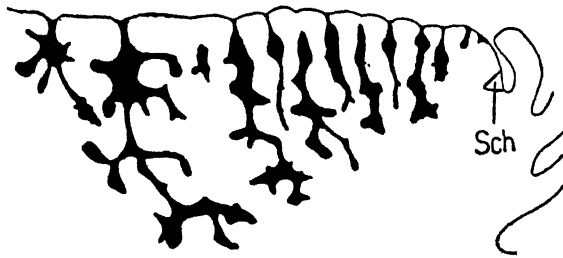


FIG. 15.

Plagiochasma renatum (after Orth). Origin of the complex air-chambers by splitting. Sch, apical cell; to the right of it scales, to the left the darkly shaded air-chambers. (From Von Goebel.)

time ; usually the splitting begins externally, and the opening is present from the first, but in *Marchantia* and *Preissia* it begins internally. Further, the difference in origin of the photosynthetic tissue is not so essential as it might at first appear to be. Speaking teleologically, the chambering tends to uphold the area of inner presentation-surface in the massive thallus.¹

Thus constituted the thallus may attain considerable size, and it is capable of living in exposed situations : some types are even specialised for life under conditions of temporary drought. On the other hand certain genera live in moist situations, and show various degrees of hygrophilous simplification. For instance, in *Cyathodium*, while the chambered structure on the upper surface is maintained, with a simple air-pore for each chamber, the tissue below is represented only by a single layer of cells, and the usual assimilating cells are absent from the cavities. On the other hand, in *Dumortiera*, it is the chambered structure that is reduced, though this is sometimes represented by rudimentary outlines that indicate the margins of the cavities, as in *Dumortiera velutina*. But sometimes even these are absent, a state which is seen in the fleshy but simple thallus of *Monoselenium*. Thus

¹ This paragraph is a free translation from Von Goebel's *Organographie*, iii. Aufl., Teil ii., p. 749. See also Orth, *Flora.*, Bd. 124, 1929, where the literature is cited.

the thallus of the *Marchantia*-type may be degraded to a state comparable with that of the thalloid Jungermanniaceae. Lastly, in the Ricciaceae the air-chambers appear still present, but greatly reduced in width, as deep narrow channels formed by splitting of cell-walls. In *Euriccia* there are no complications of structure where they open to the air, except some enlargement of the boundary cells. In fact the pores remain here at the first stage of development as seen in *Marchantia*. But intermediate steps between this state and that of *Marchantia* are found in the sub-genus *Ricciella*. Thus there may be recognised three distinct types of hygrophilous reduction all referable in origin to the structure seen in its most elaborate form in *Marchantia* or *Preissia*, viz., that typified by *Cyathodium*, that of *Monoselenium*, and that of *Euriccia*.

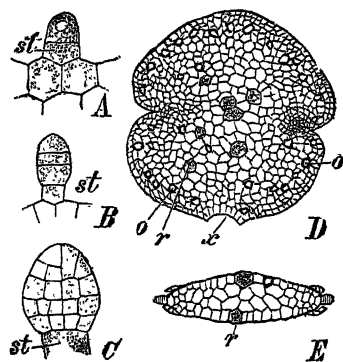


FIG. 16.

Marchantia polymorpha. a-c, successive stages in the formation of a gemma; st, stalk-cell; D, surface view; E, transverse section of an adult gemma; x, point of attachment to stalk; o, oil cells; r, colourless-cells with granular contents, from which the rhizoids will develop. A-C, $\times 275$; D-E, $\times 65$. (After Kny, from Strasburger.)

Lastly, certain of the Ricciaceae have a floating habit, as in *R. natans*; others may have a wholly submerged habit, as in *R. fluitans*. Either of these may also grow on land, when the thallus takes a more compact form: when submerged sexual organs are not formed. The thallus is chambered and pores are present in either case, but in the submerged forms the pores are closed, though in the land forms they are open. Such hygrophilous forms of Liverworts have often been adduced as evidence of an aquatic origin for the Class. But Von Goebel suggests it as more probable that the relation of the submerged

Liverworts to those that are subaerial is like that of aquatic Sced Plants to the Land Vegetation.

The amphigastria, or ventral scales, which overlap the growing point, appear in the adult region as rows of scales on either side of the midrib, upon the lower surface of the thallus. In their simplest form they are mere mucilage-papillae, but they may widen out into cell-surfaces, and may even contain chlorophyll, as in *Riella*, and assume a leaf-like appearance. Their primary function is, however, protection for the apex (Von Goebel, *l.c.*, p. 709). It suffices here to mention briefly the gemmae which are so characteristic as organs of vegetative propagation in *Marchantia* and allied genera. They are produced in large numbers and in long succession in the well-known gemma-cups, and may also be regarded as results of elaboration of mucilage-papillae (Fig. 16). Each is a discoid body with an indentation on either margin where apical growth is initiated. At first it is not dorsi-

ventral, but bilateral; the structural distinction of upper and lower surfaces of the thallus appears only on germination, and is induced by light. As both of the apices may develop the gemma of *Marchantia* is bivalent. The twin thalli thus produced form rhizoids from outgrowth of cells on the lower surface.

Much greater interest from the point of view of comparative morphology is presented by the sexual organs, and the parts concerned in the origin, nutrition, and protection of them and of the diplophase, or sporogonium. In the simpler types of the Marchantiales, such as the Ricciaceae, the

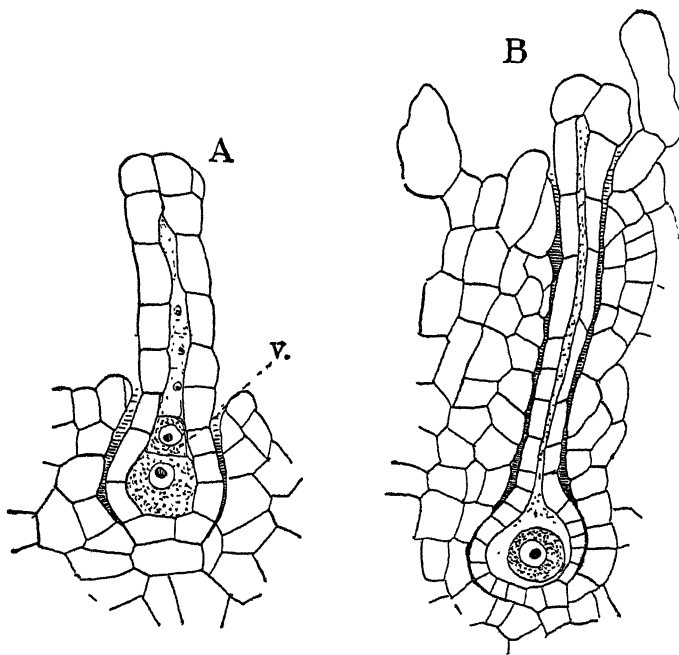


FIG. 17.

A, archegonium of *Riccia trichocarpa* showing ventral-canal-cell (v) and ovum, $\times 525$.
 B, ripe archegonium of *Riccia glauca*, $\times 260$. (After Campbell.)

antheridia and archegonia are borne in acropetal order on the upper surface of a thallus not highly specialised for the purpose. In some species the antheridia and archegonia are sunk deeply, each in separate cavities of the same monoecious thallus (Fig. 17). But in *R. natans* they are respectively segregated into groups, and related to a median ridge which is overarched by the adjoining tissue of the thallus. There are thus two grades of adjustment within the genus; nevertheless there is no high degree of specialisation of the thallus to bear the sexual organs. In contrast to this rudimentary state stand the larger types, such as *Fegatella*, *Dumortiera*, and *Marchantia*, in which branches of the thallus are specialised to form antheridiophores,

bearing antheridia deeply sunk in the exposed upper surface; or as archegoniophores of complex structure, upon which archegonia are borne; here also they arise from the morphologically upper surface, but the tip is directed downwards owing to curvature of the thallus, and elaborately protected so long as the archegonia and sporogonia are young. These branches may be variously stalked, so as to raise the antheridia when mature, or the fruits at ripeness, and thus to ensure the distribution respectively of the sperms or of the spores. Between these extremes of the simple Ricciaceae and the elaborate Marchantiaceae the Marchantiales may be ranged as a sequence, whether they be examined in respect of the structure of the vegetative thallus, or of the complexity of the branches which are specialised for sexual propagation and spore-production.

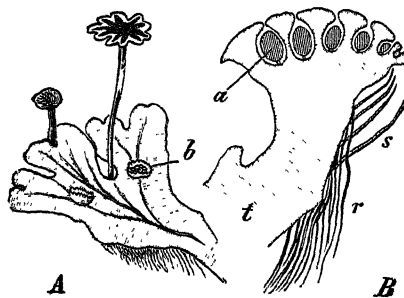


FIG. 18.

Marchantia polymorpha. A, a male plant with antheridiophores and gemma-cups, b, natural size. B, section of young antheridiophore; a, antheridia; t, thallus; s, ventral scales; r, rhizoids. Somewhat magnified. (After Strasburger.)

The mature antheridiophore of *Marchantia polymorpha* appears as a distal lobed disc, borne upon a stalk; a growing point lies at the end of each ray. The disc is formed symmetrically right and left of a median line; ventral scales are present on the under surface. It is clearly the result of repeated localised dichotomies, producing usually eight to ten rays: but in other species there may be two forkings or only one, giving smaller numbers of rays. The antheridia

are seated each in a separate superficial hollow, and as they are formed in acropetal succession the supply of sperms is long continued. The antheridiophore is thus a specialised and stalked branch-system of the thallus, with antheridia sunk individually into its upper surface (Fig. 18).

The archegoniophore of *M. polymorpha* is also stellate; here, however, the rays are not themselves branches of the thallus, but products of middle-lobes of the dichotomous system. The number of rays is usually nine, and between them lie the actual results of dichotomy, with their apices turned strongly downwards, and incurved towards the supporting stalk: this remains short at first, but it lengthens as the fruits ripen, giving the well-known stellate archegoniophore. A vertical section traversing one of the growing points (S) will demonstrate the acropetal succession of the archegonia borne on the convex upper surface of the thallus, which is chambered as usual (Z, Fig. 19). It also shows the orientation of an archegonium approaching maturity, with its neck directed upwards, a position readily receptive for sperms conveyed by water dripped or splashed upon the still sessile archegoniophore, from the taller-stalked antheridiophores.

The gametangia of the Marchantiales present features of segmentation which are general for the Liverworts, though here presented on a relatively

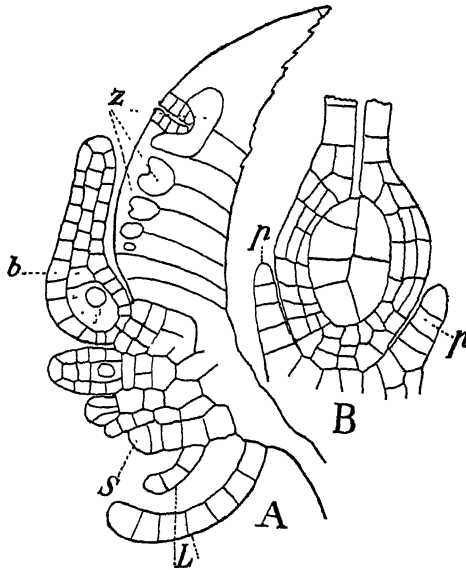


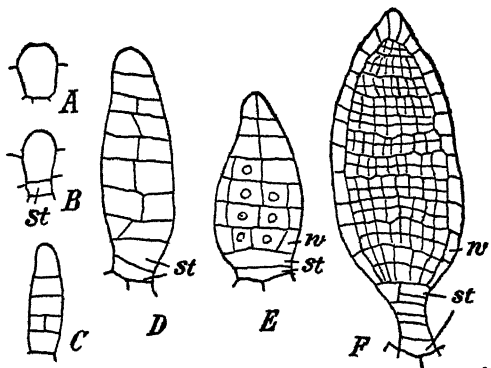
FIG. 19.

Longitudinal section through a young archegoniophore of *Marchantia polymorpha*. It is seen that the archegonia originate on the upper side. *S*, apical cell of the shoot; *b*, ventral canal-cell of the oldest archegonium; *L*, ventral scales; *B*, longitudinal section through a fertilized archegonium of *Preissia commutata* with embryo of few cells only; *p*, perianth. (After Von Goebel.)

large scale. The micro-gametangia (antheridia) are club-shaped, consisting of a short stalk (*st*), bearing distally a mass of spermatocytes covered by a

single layer of the protective wall (*w*, Fig. 19, *bis*). Each antheridium arises from a single cell (*A*), which divides by parallel cleavages (*B*, *c*), to form successive tiers of cells that result from quadrant-division in each (*C*, *D*), while cells of the wall (*w*) are formed by relatively late periclinal division (*E*). The inner cells divide further to form the cubical spermatocytes (*F*).

Each archegonium also springs from a single cell, in which a transverse cleavage separates a stalk (*st*) from the archegonial cell (Fig. 19, *tris*, 1). By longitudinal cleavages in

FIG. 19, *bis*.

Stages of development of the antheridium in *Fegatella*. (After Bolleter, from Von Goebel, *Organographie*, 3rd Ed., p. 145. For description see text.)

the latter three sterile cells are defined surrounding a middle fertile cell (2). In this a transverse cleavage separates the cap-cell (3, *d*), from an inner cell which is the central cell. It is followed by a further transverse cleavage of the latter, giving rise to an outer cell (*h*) and an inner cell (*c*, Fig. 19, *tris*, 4). The former after further transverse cleavages produces the canal-cells, the latter, by a further transverse cleavage, gives the ventral canal-cell (*b*, Fig. 19), and the ovum. Meanwhile transverse and longitudinal divisions of the outer sterile cells will have produced the archegonial wall and neck, upon the end of which is the distal rosette that results from repeated divisions of the cap-cell.

Von Goebel holds that the antheridia and archegonia, as shown by comparison of their development, are homologous parts, which originated from a

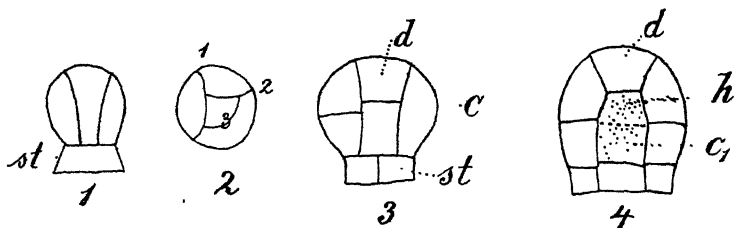


FIG. 19, *tris*.

Diagram of archegonial development in Liverworts. 1, 3, 4, in longitudinal, 2, in transverse section. In 3 the inner cell and the cap-cell (*d*) are separated. In 4 the inner cell has again divided. *st*=stalk. *h*=parent of canal-cells. *c*₁=parent of *v*, *c*, *c*₁ and ovum. (From Von Goebel, *l.c.*, p. 147.)

common source. The further discussion of these organs from this point of view will be taken up in Chapter XXV.

The protections of the archegonia call for notice, as they have been brought afresh into morphological comparison. The individual archegonium of *Marchantia* is surrounded by a covering called the perianth, which arises after fertilisation at the base of the venter (*p*, *p*, Fig. 19, B); it forms at first a close investment of the young fruit. There is also a pendent curtain, called the perichaetium, which has a fimbriated margin. It takes the form of opposed flaps which enclose not only one archegonium but a number of them. Such a development is present in all of the more elaborate Marchantiales, and also in the thalloid Jungermanniales: thus the perichaetium is a relatively constant feature. The perianth is, however, less constant; for instance, it is wanting in *Dumortiera*. The elaborate structural arrangements thus seen in *Marchantia* are such as will tend to secure the following ends, viz., the distribution of the sperms with high probability of fertilisation, and a lengthened period during which fertilisation is possible; the production of a plurality of sporogonia in relation to each ray of the archegoniophore, and effective protection of the young sporogonia, with ready distribution of the spores when mature.

Within the Marchantiales there is considerable variety in detail of the grouping and protection of the sexual organs. The genera may be seriated according to their complexity or simplicity. For a detailed exposition of the facts, which would be out of place here, reference should be made to Von Goebel's *Organographie* (iii. Aufl., Teil ii., pp. 831-840). After discussing whether the genera may constitute an ascending or a descending series his conclusion is as follows. The position of the gametangia and the development of the thallus-branches that bear them is originally the same. Starting from the gametangiophores (Träger) as seen in *Marchantia*, a series of simplification may be readily followed. The fertile branches tend to lose their individuality, first the male and then the female, so that the gametangia appear to be scattered over the surface of the thallus, as they are in *Riccia*. Sheaths of two kinds are present, the "perianths" which appear as individual sheaths, dependent or not upon fertilisation for their further development, and "perichaetia," which ensheath groups of archegonia; the thallus itself together with a dorsal growth from the thallus co-operate in producing the latter. The appearance of perichaetia has in many forms made a reduction of the perianth possible; nevertheless Von Goebel regards the perichaetia as of secondary origin. Elsewhere he remarks that those of the *Marchantiales* in which a perianth is present are to be regarded as the more primitive, a special reason being that in them the male and female gametangia correspond in their sheathing—a fact found in *Sphaerocarpus* (*l.c.*, p. 830). The validity of this series of reduction will be considered later, where other evidence will be available (see p. 40).

THE SPOROAGONIUM

Passing now to the diplophase, or sporogonium of the Marchantiales, there is a strong contrast between this and the haplophase. The difference is much more marked than in the Anthocerotales. Not only is the form of the two phases more distinct in the Marchantiales, the gametophyte being dorsiventral and the sporophyte radially constructed, but they differ also in respect of photosynthesis, the one bearing chlorophyll and being amply ventilated in the larger forms, the other being incapable of self-nutrition and solid. The sporophyte is in fact a specialised body nourished from the parent thallus, and engaged wholly in the production and dispersal of spores. Its form varies from the spherical, as seen in *Riccia*, to oval or cylindrical variants with marked polarity, as in most of the representatives of the order. The apex is directed towards the neck of the archegonium, while the base is deeply inserted in the tissue of the gametophyte. The embryogeny is thus exoscopic, as it is in all Bryophytes. The archegonium is persistent: though the neck shrivels after fertilisation it can long be recognised, while

the venter expands as a close investment over the growing sporogonium, and is known as the calyptra.

The drawings of Cavers of successive stages of development of the sporogonium in *Fegatella conica* give the essential features for one of the larger Marchantiales (Fig. 20). They also show its relation to the arche-

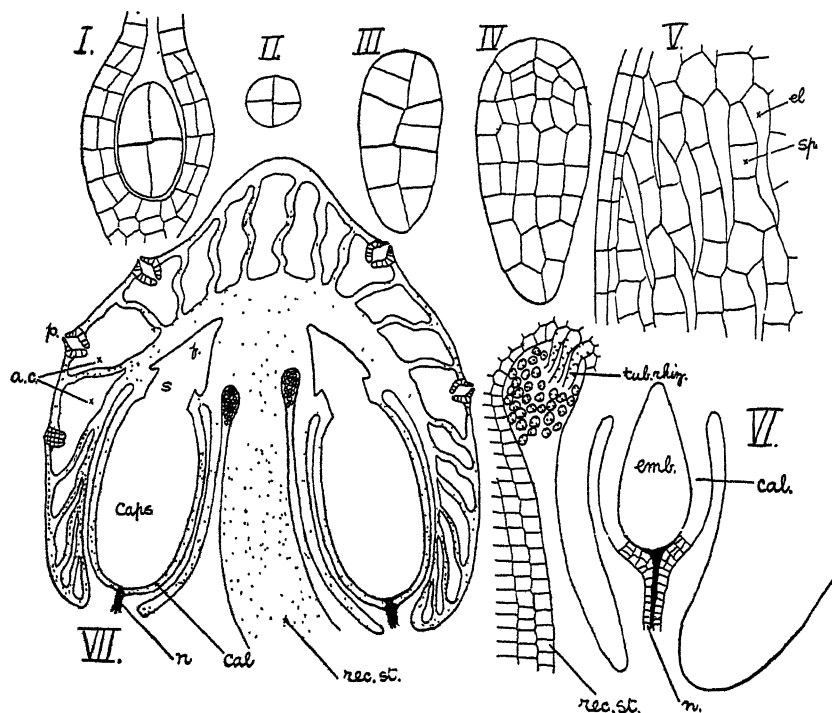


FIG. 20.

Sporogonium of *Fegatella (Conocephalus)*. I., venter of fertilised archegonium with eight-celled embryo. II., transverse section of a similar embryo. III., IV., older embryos in longitudinal section. V., part of a longitudinal section of a developing capsule, showing differentiation of archesporial tissue into elater-forming cells (*el*), and sporogenous cells (*sp*). VI., part of longitudinal section of receptacle with embryo. VII., similar section showing two mature sporogonia in outline. *ac*=air-chambers; *cal*=calyptra; *caps*=capsule; *f*=foot; *n*=neck of archegonium; *p*=pore; *rec. st.*=stalk of receptacle; *rhiz.*=rhizoids; *s*=seta of sporogonium. I.-V. $\times 360$. VI. $\times 76$. VII. $\times 20$. (After Cavers.)

goniophore (see Cavers, *Ann. of Bot.*, xviii., 1903, p. 87). The figures I-V are orientated with the apex upwards, VI and VII downwards. The first cleavage of the zygote is in a plane transverse to the axis of the archegonium (I, III); it stamps the polarity of the embryo, and delimits the epibasal and hypobasal regions. As a rule the next cleavages divide the embryo into octants. Meanwhile it grows vigorously in length, the upper region giving rise to the stalk and capsule, the lower to the foot, which ultimately takes a spear-head form (VII). In the upper region the outer layer gives rise to the

double wall of the capsule (IV, V) ; the inner cells form the archesporium, from which spores and elaters are produced. The archesporial cells are at first all alike, but later they become differentiated into two kinds which show no definite relation to each other beyond a tendency to arrangement in longitudinal rows (V). Some of them elongate and remain narrow, others grow equally in all directions, and contain dense protoplasm. The former produce elaters which are often branched, and have spirally thickened walls ;

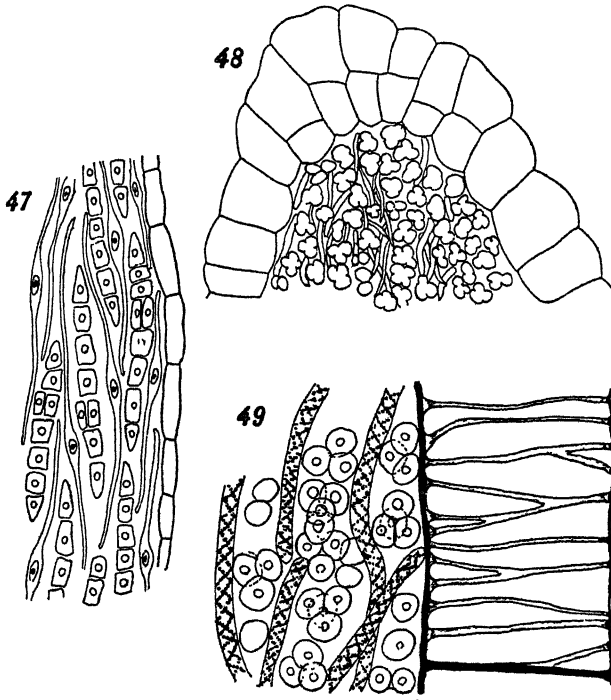


FIG. 21.

Monoclea Forsteri, Hook. 47=part of a longitudinal section of a capsule, showing elaters and rows of spore-mother-cells. $\times 350$. 48=longitudinal section of the tip of a nearly mature capsule, showing the lobed spore-mother-cells. $\times 160$. 49=elaters, tetrads of spores, and a cell from the wall of a still more mature capsule. $\times 350$. (After Johnson.)

the latter become rounded off as spore-mother-cells, and after tetrad-division in the manner of Liverworts they form spores. This is here illustrated by Johnson's drawings from *Monoclea* (Fig. 21). At the extreme tip of the capsule there is, as a frequent feature of the Marchantiales, a well-marked cap of cells in several layers, which projects into the cavity. It is seen in *Cyathodium* (Fig. 22), and it originates from the archesporium. In *Fegatella* a few elaters are attached to it, while others are similarly fixed at the base of the cavity. At ripeness the apical cap separates along an irregular line of cleavage, and this is followed by longitudinal

fission along four to six lines. Meanwhile the seta elongates, and the ruptured capsule with its spores and elaters is exposed.

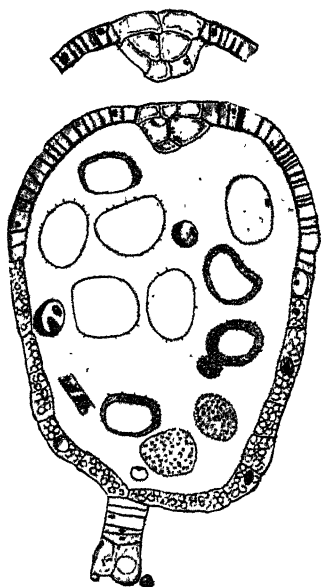


FIG. 22.

Cyathodium cavernarum, longitudinal section of an almost mature sporogonium showing apical disc. $\times 200$. Above, the apical disc of the same sporogonium in median section. $\times 200$. (After Lang.)

becomes obliterated later, as also does the inner layer of the calyptra, so that the spores lie practically free in the cavity surrounded only by the outer layer of cells of the calyptra.

Such types as *Marchantia* and *Fegatella* on the one hand, and *Riccia* on the other, represent extremes of sporogonial development in the Marchantiales. Between them other intermediate examples may be ranged, and the series may be held as naturally related, since all show essentially similar methods of development and of final result. They diverge in certain features, particularly in the degree in which structure marks polarity. In the larger and more elaborate the apex and base of the sporogonium are distinct

This description will serve for the more elaborate sporogonia of the Marchantiales. For comparison and contrast an account may be given of the simple capsule of *Riccia* (see Campbell, *Mosses and Ferns*, edn. iii., p. 33). The early segmentation of the zygote is in essentials like that in *Fegatella*, and other Marchantiales. But polarity is not defined by its external form. A superficial wall is soon formed by periclinal cleavages, but it remains a single layer. The whole of the enclosed cells develop as an archesporium, and all serve as spore-mother-cells, which round off and undergo tetrad-division. Meanwhile the cells of the venter of the archegonium have divided to form the two layers of the calyptra. Fig. 23 shows the structure as seen in *Ricciocarpus natans* at the period when the spore-mother-cells separate; it also shows the single-layered wall, which

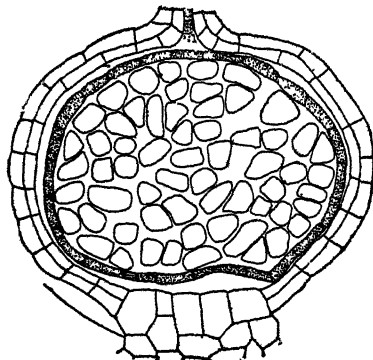


FIG. 23.

Ricciocarpus natans. Young sporogonium in longitudinal section, surrounded by the archegonial wall. It shows the amphithecium (shaded) surrounding the sporogenous cells already separated, as the free, and rounded spore-mother-cells. $\times 560$. (After Garber.)

structurally and functionally. The polarity is exoscopic, and it is marked by the first cleavage of the zygote, which separates the hypobasal and the epibasal regions. Later the foot and seta develop as markedly distinct from the epibasal capsule. This result appears to be independent of geotropic influence. Though in *Marchantia* the archegonium is seen to be directed upwards at the time of fertilisation (Fig. 19), it is turned downwards during embryogeny. More detailed observation will be necessary for a final decision of the point. In the smaller and less elaborate spherical sporogonia of the Ricciaceae the polarity cannot be recognised, unless it be by the first cleavage of the zygote, which is approximately transverse to the axis of the archegonium. There is no foot or seta and, as we have seen, all the cells within the single layer of the wall are fertile, whether of the epibasal or of the hypobasal regions. But in the larger forms they do not all prove fertile, as they are in *Riccia*. A distinction arises between the spore-mother-cells and the elaters. The final function of these in the larger types is to assist mechanically in the dispersal of spores, but it is possible that in such a plant as *Fegatella* they may in some degree aid also in the nutrition of the cells which are fertile. This seems undoubtedly to be the case in *Corsinia*, and in certain other genera of doubtful affinity, such as *Sphaerocarpus*, and *Riella*, for here the sterile cells are not mechanically strengthened by spiral or annular thickening of the walls. They are recognised as "nutritive cells"; they appear to aid in nourishment, perhaps also in dispersal of the spores by swelling of their mucilaginous remains. Lastly, in the larger Marchantiales there is regularly present, at the distal end of the capsule, that small mass of tissue already mentioned within the wall, which remains sterile and comes away at dehiscence as a cap or lid (Fig. 22). In *Fegatella* a similar mass of cells serves as the point of attachment for some of the elaters, while at the base there is a like attachment of some of them to the sterile seta (Cavers, *l.c.*, Fig. 48).

Using facts of this nature it is possible to lay out the Marchantiales in series according to the complexity of the sporogonial structure, ranging them between the simplest, such as *Riccia*, and the most elaborate, such as *Marchantia* and *Fegatella*. The argument has been propounded that, so seriated, they illustrate a natural advance based upon progressive sterilisation of potentially fertile cells, these being diverted from their original function of spore-production to somatic functions in relation to the nutrition and disposal of the spores. This theory of sterilisation was applied to the Marchantiales in *The Origin of a Land Flora* (1908, pp. 257-263). It was further elaborated by Cavers ("Inter-relationships of the Bryophyta," *New Phytol.*, Reprint No. 4, 1911, pp. 49-62). It appeared to bear the impress of biological probability, though it was based primarily upon the features of the diplophase alone. Before it can be accepted it would appear desirable, and

indeed obligatory, to bring the facts drawn from the preponderant haplo-phase also into the comparison. Thus a wider scope would be given to the argument, or perhaps a corrective might be applied. This has been done by Von Goebel (*Organographie*, iii. Aufl., Teil ii., pp. 389, etc., and 760-767). The chief results which emerge from his very wide comparisons are, first, that there is widespread evidence of reduction shown in the vegetative characters of the gametophyte of the Marchantiales; secondly, the fact that such reduction runs parallel with simplification, both in the parts which bear and protect the sexual organs and in the structure of the sporogonia which they produce. Such evidence seems to discount that favouring the suggested advance of the sporophyte. To arrive at a just judgment in such questions the widest possible area of comparison will be necessary. Not only should the particular sequence under review be canvassed, but others also of related type. Hence, for the present, we must be content to have recognised that the Marchantiales constitute a sequence which raises this evolutionary problem, though the balance of probability seems now to point to the simpler types having resulted from reduction in both of their alternating phases, rather than as being themselves primitive.

Though no comparative measurements of the Marchantiales have been submitted here as evidence, it is apparent that the complexity of structure of their chambered thallus is high in those of large size and relatively exposed habit; in those of moist habitat that structure may be imperfectly developed, or even absent. The reductions studied comparatively by Von Goebel are most marked in genera and species of damp or even of aquatic habit. Whether the actual origin of the chambered structure be by fission of cell-walls or by involution of the surface, or by both combined, the result is the same, viz., that the massive thallus is ventilated in the region where it is photosynthetic, while the gaseous interchange is more or less controlled by pores analogous, though not exactly similar in origin or effectiveness, to that of the stomata of ordinary land-vegetation. The effect of the chambered structure is to tend to maintain the presentation-surfaces, and so to facilitate or control gaseous interchange. Naturally this will be most necessary where the size is relatively great. The most marked structural character of the Marchantiales, viz., the chambered thallus, may thus be recognised as a biological adjustment in relation to size and habit.

Elaboration of external form by foliar development is, however, a more familiar method of meeting the biological difficulty of increasing size. In ordinary land-vegetation this is commonly combined with internal ventilation by intercellular spaces and stomata, but this is no necessary relation. In the Jungermanniales, which will be discussed in the next Chapter, foliar development will be seen as an alternative to the internal ventilation of the thalloid Marchantiales. It appears that the two Orders have diverged structurally, by holding firmly either to the one or to the other of these two methods of main-

taining the presentation-surfaces of their gametophytes. But in the sporophytic leaves of ordinary land-vegetation those two methods are combined, and the biological advantage that ventilated leaves possess is witnessed by their still greater size and elaboration, as seen in the Pteridophytes and Seed Plants.

CHAPTER III

JUNGERMANNIALES ¹

THIS Order includes those Liverworts which have exploited most fully the foliar development of the haplophase or gametophyte. The interest in this is enhanced by the fact that the Order includes also thalloid forms and that, by steps which may be compared, a transition may be traced between the latter and the leafy types. The general life-history is essentially the same as in other Liverworts, though the details of the gametangia differ, as also of the

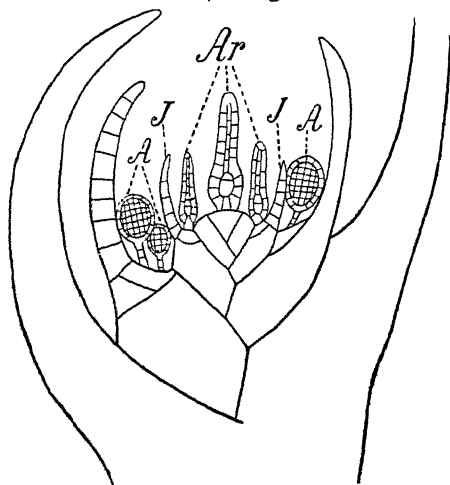


FIG. 24.

Scheme for the disposition of the sexual organs in an Acrogynous *Jungermannia*. The antheridia (*A*) are axillary, also the lower Archegonia (*Ar*). The uppermost arise with abortion of the leaf-formation, and even from the apical cell itself. (After Von Goebel.)

sporogonia, and of their nursing to maturity. Thus they form a natural group, distinct from though related to the Marchantiales and Anthocerotales.

The Order was divided by Leitgeb into two series distinguished by the relation of the archegonia to the apical cell. In one series, which includes those of thalloid construction though often showing foliar developments of a rudimentary type, the apex itself is not terminated by an archegonium, all of these being lateral and borne upon the upper surface. This series is designated the Anacrogynae, and they may be held as the

more primitive. In the second series, styled the Acrogynae, the foliar development is of a more advanced type. Here the leaves are commonly divided into two separate lobes: moreover, the apical growth of the axis is

¹ *Selected Literature on Jungermanniales*: Schiffner, *Natürl. Pflanzenfam.*, Teil i., Abth. 3, 1909, pp. 38-134. Cavers, *New Phyt.*, Reprint 15, chaps. iii., iv., where the literature is fully quoted. Grün, *Treubia insignis*, *Flora.*, Bd. 106, 1914, p. 331. Campbell, *Mosses and Ferns*, 1918, chap. iii. Walton, "Carboniferous Bryophyta," *Ann. of Bot.*, vol. xxxix., 1925; vol. xlii., 1928. Von Goebel, *Organographie*, iii. Aufl., Teil ii., 1930; Zweiter Abschnitt, "Lebermoose." Verdoorn, *Manual of Bryology*, 1932. Rayner, "Mycorrhiza," *New Phyt.*, Reprint 15, chap. ix., where the literature on fungal relations is quoted.

arrested by the formation of a terminal archegonium, with which others may be associated (Fig. 24). By these and other features they are recognised as relatively advanced in organisation. This series is represented by a very large number of genera and species, both in cold climates and in the tropics. The distinction, however convenient for descriptive purposes, does not follow precise lines. For instance, the primary leaves of *Acrogynous* sporelings are often "simple," like those of the *Anacrogynae*. Thus we may say that, in an early stage for the most part quickly passed over, the leaf-formation of the *Acrogynae* is comparable with that of the *Anacrogynae* (Goebel, *l.c.*, pp. 723-4). Again, the phyletic shifting of the archegonia towards the apex is a general feature of advance, and is illustrated also among the *Anacrogynae*, though in them the actual initial cell is not involved. Moreover, analogies may be pointed out in either series in the steps leading towards foliar differentiation, which may be traced, here as elsewhere, along homoplastic lines. Thus it may be held that the Jungermanniales as a whole form a very natural sequence, in which foliar development has materially contributed to its success, as measured by the number of living genera and species.

In many *Anacrogynous* Liverworts a simple dorsiventral thallus is seen. In *Pellia* it appears as a flat green expanse with smooth upper surface, a sinuous margin, and slightly thickened midrib. It branches frequently by dichotomy, but with sympodial development. Amphigastria are absent, but numerous rhizoids spring from the lower surface. It consists of almost uniform chlorophyll-bearing cells, and is more massive along the median line, where the cell-walls are sometimes strengthened by brown bars of thickening, but it thins out to a single layer at the margins. *Aneura* is more elongated, as is also *Metzgeria*, where there is a distinct midrib with flange-like wings, and dichotomy is a repeated feature of the narrow thallus. Superficial hairs are present in some species, particularly on the calyptra. The genera above-named are among the simplest *Anacrogynous* Liverworts as regards the

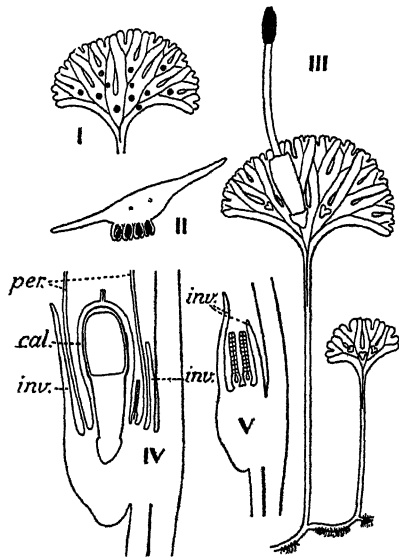


FIG. 25.

Umbraculum (Hymenophyllum) flabellatum. I. Part of a male plant from below, showing the antheridial branches (diagrammatic); II. Cross-section of a male plant, showing the antheridia; III. Part of a female plant, with archegonial branches, and a sporogonium; IV. Longitudinal section of an archegonial branch with a nearly ripe sporogonium; V. Similar section of a branch with unfertilised archegonia. *cal*, calyptra; *inv*, involucre; *per*, perianth. (After Cavers.)

thallus. But in certain genera a higher organisation of the vegetative system may arise through differentiation of the branches, so that a remote comparison might be drawn with the external organisation of vascular plants. This is seen in *Symphyogyna*, or *Hymenophyllum* (Fig. 25). In the latter a lower flangeless region is attached root-like to the soil by rhizoids; a flangeless upright stalk bears erect a dichotomously branched system of winged thalli, while upon the dorsal surface the sexual branchlets are produced, with antheridia and archegonia, and finally the sporogonium.

On the other hand, elaboration of structure of the individual winged thallus of the *Anacrogynae* may also play its part. The broad flanges may

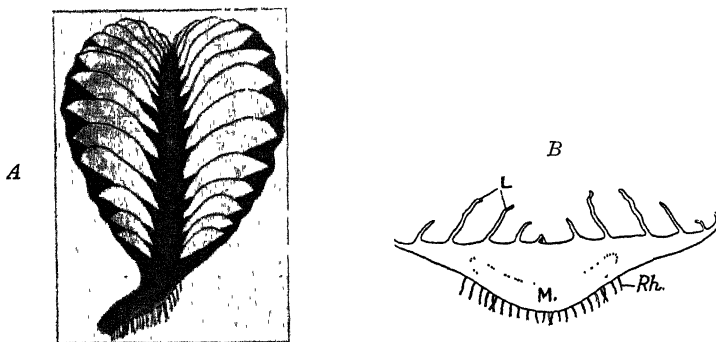


FIG. 26.

Petalophyllum ralfsii. A. Plant as seen from above. $\times 8$. B. Transverse section through the middle of the leaf-bearing region of the plant. $\times 20$. L, leaves; M, mycorrhiza; Rh, rhizoids. (After Cavers.)

be waved like the margins of a "goffered" curtain, thereby greatly increasing the surface exposure, as is seen in *Mörckia* (Cavers, *l.c.*, Fig. 32). Or they may be partially or completely dissected by involutions of the margin, so as to form lobes more or less distinct, as in *Symphyogyna*. Secondary flanges may even arise, as surface outgrowths from the primary flanges, as in *Petalophyllum ralfsii*; this greatly enhances the efficiency of the photosynthetic system (Fig. 26).

Others again may actually attain a foliar habit, as is seen in *Treubia*, described by Von Goebel,¹ which is the largest of all of them, having distinct leaves, each 1 cm. in length. These are borne in two lateral rows, with oblique insertion on the axis, which has a three-sided apical cell; but there is no trace of ventral appendages. The leaves consist of several layers of cells at the base, but distally of only a single layer; they are "succubous," that is, the anterior margin of each is covered by the posterior margin of the next higher leaf. Each leaf of *Treubia* bears a flap which appears to arise from its upper surface; these flaps are formed early, and together they protect the growing point and the sex-organs; hence ventral appendages are not neces-

¹ *Organographie*, p. 717; also Grün, *Flora.*, 106, p. 331.

sary. The foliage of *Treubia* thus appears to approach that of the Acrogynous Liverworts (Fig. 27).

Lastly, there remains the little family of the Calobryaceae, which have tristichous leafy shoots, rising erect from underground rhizomes devoid of rhizoids. There is a three-sided pyramidal apical cell, around which the sexual organs are grouped. *Calobryum* and *Haplomitrium* stand alone

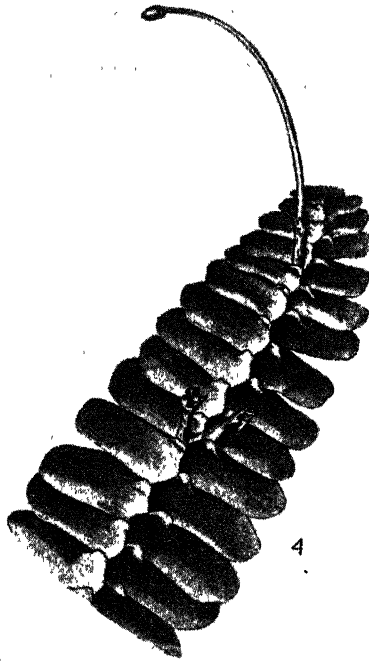


FIG. 27

Treubia insignis, Goebel. 4, young plant of *Treubia* with sporogonia, two young and one ripe; the spore-capsule is borne on a long stalk. Natural size. (After Grün.)

among Liverworts in having radial orthotropic shoots. Further, they have neither Perianth nor Perichaetium.

The Acrogynous Jungermanniales include still more elaborate vegetative types, many of which are of epiphytic habit. The leaves are arranged in three rows, coinciding with the segmentation of the three-sided apical cell. Two of the rows are lateral and symmetric, the third row is ventral and unsymmetric (amphigastria); this difference may, however, be lost in orthotropic shoots. On the other hand, the amphigastria may be rudimentary or even absent, as in *Radula*; or be replaced by a cell-plate that bears rhizoids, as in *Leptocolea* (Goebel, *l.c.*, Fig. 718). The leaves are usually only one layer of cells in thickness, and have no midrib. A marked characteristic of the dorsal leaves, which distinguishes them from those of the Anacrogynae,

is an early division into two halves, leading when mature to a bi-lobed form ; but this is not seen in the amphigastria. The halves often differ from one another in size and in form, and they are liable to modification to subserve special functions (Fig. 28). As extreme examples two may suffice. In *Frullania* the downward-directed half develops as a water-sac or pitcher, effective in collecting and holding water in this epiphytic or rock-dwelling

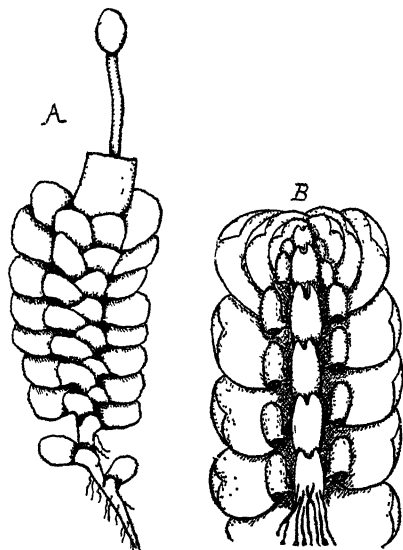


FIG. 28.

A, *Scapania nemorosa*, dorsal view of the leafy shoot, which bears a sporogonium at its tip. *B*, *Frullania tamarisci*, view of a leafy shoot from below, to show the ventral row of leaves, and the two lateral rows, of which the lower lobes bear pitchers. *A* has the undershot or "succubous," and *B* the overshot or "incubous" disposition of the leaves. (After Cavers.)

genus (Fig. 28, B). On the other hand, in *Trichocolea* the leaves may be divided into narrow branched laciniae, which collectively hold water, as in a sponge. There is, in fact, a wide scale of adaptation in the leaves of these Liverworts, offering analogies with what is seen in the sporophytic leaves of Flowering Plants. They may even be heterophyllous, and be ranged as foliage leaves, scales, and bracts.¹

The young stages from the sporeling onwards throw light upon the relation of the thalloid to the leafy state in Liverworts. Some of those which possess a highly organised and leafy sexual shoot have a preliminary vegetative phase, which is of simple construction. This may be either flattened and thalloid, with a midrib as in *Pteropsiella*, or without one, as in *Lejeunia metageriopsis* (Fig. 29);

or it may be filamentous like the protonema of a Moss, but with transverse septa, as in *Protocephalozia* (Fig. 30). It is important to note that these are merely vegetative phases of youth. When the sexual organs are to be formed the development becomes more complex, and leafy buds appear, which bear the antheridia and archegonia (Fig. 29, *b*). Two alternative views are possible in interpreting such facts. Having laid out the examples serially according to complexity, the series may be read from an evolutionary aspect, either from thalloid to foliose, as an advancing series ; or from foliose to thalloid, as a series of reduction. The first inclination would probably be to adopt the former view, and so long as we envisage the individual rather than the race the facts would suggest a progression such

¹ For further details as to these reference may be made to special treatises, and particularly to Goebel's *Organographie*, iii. Aufl., pp. 720-794.

as the individual life seems to depict: the ontogeny providing the phylogenetic steps. But if a wider view be taken, based upon the race rather than

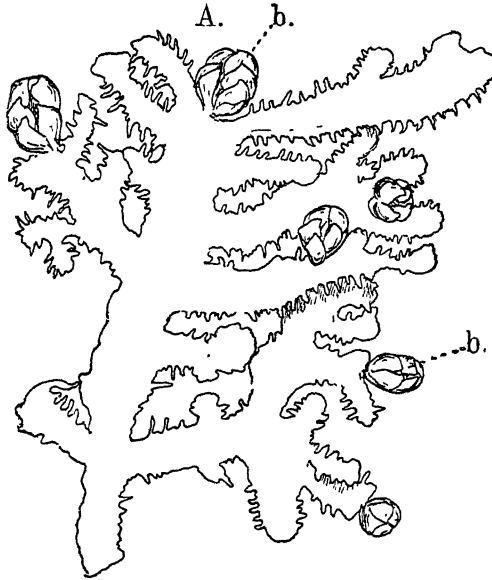


FIG. 29.

Lycopodium metzgeriopsis, showing the thalloid protonema with terminal leafy buds (b).
× 14. (After Von Goebel, from Campbell.)

on the individual, a converse reading of the facts is possible; viz., that in accordance with the conditions the race may have suffered reduction. On

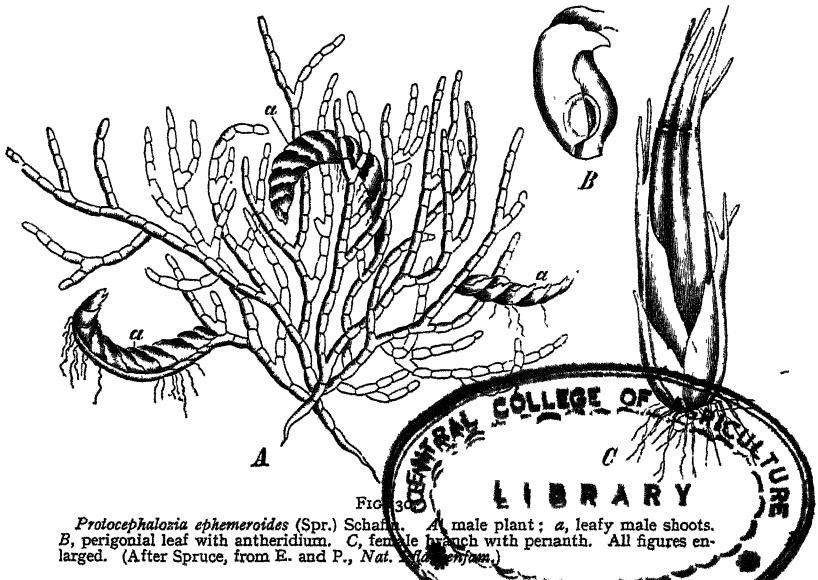


FIG. 30.

Protocephalosia ephemeroidea (Spr.) Schaef. A, male plant; a, leafy male shoots. B, perigonal leaf with antheridium. C, female branch with perianth. All figures enlarged. (After Spruce, from E. and P., *Nat. Hist. Japan*.)

this question, and provisionally, the opinion of Von Goebel may be quoted, viz., that there are Acrogynous leafy Liverworts which sink to a simpler, partially or completely thallose conformation. This may come about in various ways. But the sexual shoots always retain the typical foliar state, indicating that the form of the vegetative organs, which thus approaches to the thalloid state, is one of secondary origin. We should not, however, be justified in adopting any general derivation of thalloid from foliose forms (Goebel, *l.c.*, p. 739). On this point our own opinion may meanwhile be held in suspense until the question is taken up again with a more general application (see p. 56).

Vegetative propagation of the Jungermanniales is carried out by gemmae of various size and form. These are of little importance for morphological

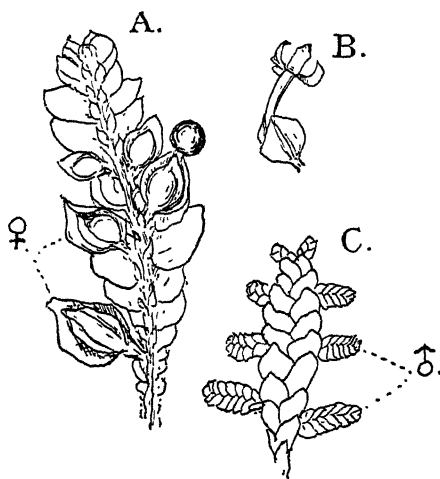


FIG. 31.

Porella Bolanderi. A, female plant, with archegonial branches. B, an open sporogonium. C, a male plant, with antheridial branches. $\times 4$. (After Campbell.)

comparison. It may suffice to remark that those of *Aneura* have attained some notoriety, owing to the fact that they are two-celled and endogenous; they slip out from the superficial parent cells, owing to a mucilaginous change of the middle-lamella of their walls; but they appear never to be naked protoplasts, and they possess no cilia: this vitiates the suggested comparison with algal zoospores.

As an example of the sex-organs of average leafy Liverworts those of *Porella* will serve; they are similar in essential points, though not in detail, to those of other Liverworts, such as *Marchantia*. The plants are dioecious, the males being smaller than the females. The special antheridial branches bear imbricated leaves, with an antheridium at the base of each (Fig. 31, C). The antheridium arises as a single cell, which divides transversely to form the stalk and the antheridial head; the latter segments so

as to produce a single-layered wall, surrounding numerous spermatocytes within (Fig. 32 A, B). The stalk is elongated at maturity, and consists of two rows of cells, while the wall becomes 2-3 layered at the base (C) : its distal region is thinner, and ruptures on access of water, while the ragged margin is recurved, so that the biciliate sperms are liberated into the water that causes the rupture (D).

The archegonial branch is short, and only two or three leaves originate on it. After these are initiated certain of the segments of the apical cell

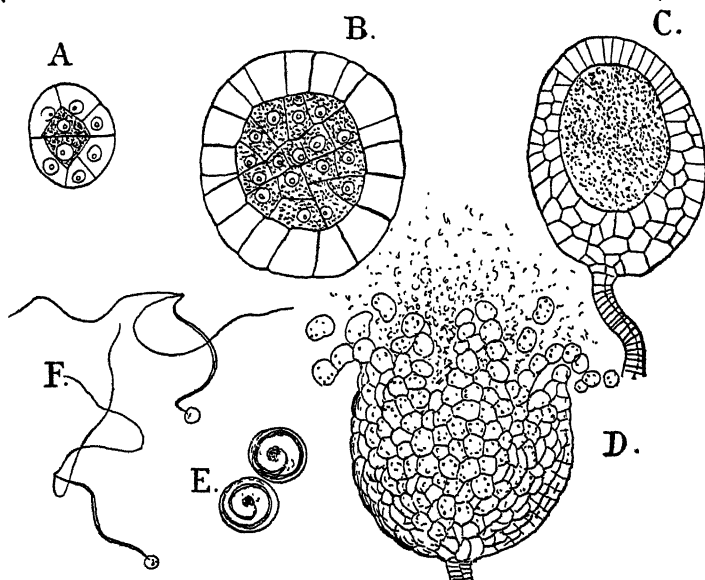


FIG. 32.

Porcella Bolanderi. A, B, cross-sections of young antheridia. $\times 600$. C, longitudinal section of a nearly ripe antheridium. $\times 100$. D, ripe antheridium in the act of opening. $\times 50$. E, F, spermatozooids. $\times 1200$. (After Campbell.)

themselves divide into a basal and a distal cell, the latter becoming the mother cell of an archegonium (Fig. 33 A). Its segmentation then follows the lines usual for Liverworts. The archegonial cell divides so as to cut off three lateral cells, of which the third is the smallest (C) ; the two larger divide again by vertical walls, but the smallest does not : thus the neck has only five rows of cells (G). The form of the cell thus surrounded varies, being sometimes square at the base (B), sometimes conical (D). The peripheral cells divide repeatedly by transverse walls : the lower part of the five rows thus produced forms the venter, the upper part the neck (E). Meanwhile the internal cell divides transversely, to form an external cap-cell and an internal cell (B). The former divides by intersecting walls to form four cover-cells ; the latter divides repeatedly to form the axial chain of canal-cells, the ventral canal-cell, and the ovum (E, F). The archegonia are formed

in acropetal order, but finally the apical cell itself is involved. These details of development of the sexual organs are of some importance for comparison

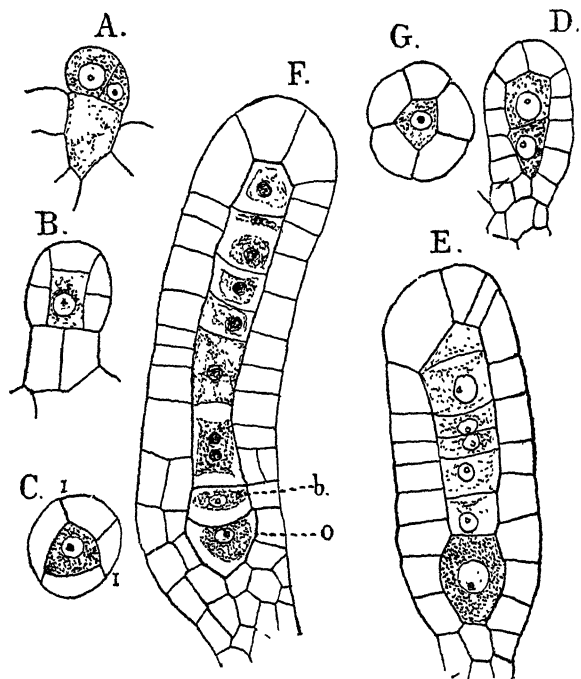


FIG. 33.

Porella Bolanderi. Development of the archegonium. $\times 600$. C, cross-section of young archegonium. G, cross-section of the neck of an older one. The others are longitudinal sections. b, ventral canal-cell; o, the egg. (After Campbell.)

with the Mosses. Later a perianth is formed enveloping the whole group of the archegonia. Its origin is independent of fertilisation, and it may surround only abortive archegonia.

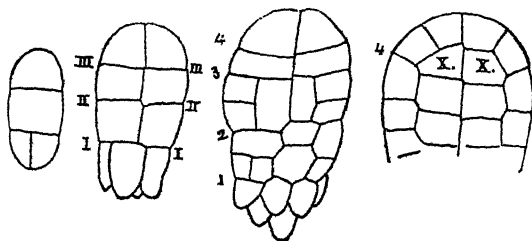


FIG. 34.

Frullania dilatata, development of the embryo. $\times 300$. (After Leitgeb.) x, x, the archesporial cells. The numbers indicate the primary transverse divisions. (From Campbell, *Mosses and Ferns*.)

After fertilisation the first segmentation of the zygote in the Jungermanniales, which is approximately transverse, separates a hypobasal from

an epibasal region, with exoscopic orientation. In some cases the former develops as a multicellular haustorium, as in *Frullania* (Fig. 34); but more frequently it remains as a minute appendage at the base of the sporogonium, either as a simple row of cells, or sometimes as a single one, for instance, in *Radula* (Fig. 35); or the basal cell may be branched without division, as in *Aneura* (Fig. 36). The epibasal region gives rise to the capsule and stalk. It undergoes more active segmentation, often with considerable regularity, so that a number of transverse discs are formed, each composed of four cells, while the terminal tier consists of four octants of a hemisphere. This uppermost tier appears to be cut off by the first transverse wall in the epibasal half of the zygote, and in many of the Acrogynous Liverworts both seta and capsule are derived from these cells, subsequent intercalary divisions in the lower half of the epibasal cell giving rise to the sterile seta. But in many of the Acrogynous Jungermanniaceae some of the lower tiers of cells also take part in the formation of the capsule: in *Radula* the number appears to be three (Fig. 35). Thus there is no general distinction between seta and capsule on the basis of the first segmentations.

On the other hand, the segmentation may often be less regular. For instance, in *Porella*, though the embryo is at first composed of a row of cells of which the lowest undergoes no further development, the subsequent divisions in these are more variable in succession than is seen in *Radula* and

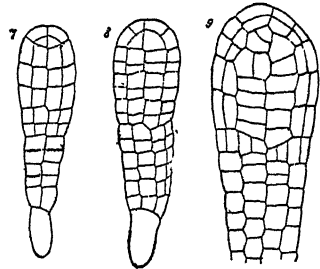


FIG. 35.
Embryos of *Radula complanata*. $\times 230$.
(After Leitgeb.) 7, 8, show the basal appendage cut off by the first segmentation of the zygote; 9, shows the upper region of a more advanced embryo.

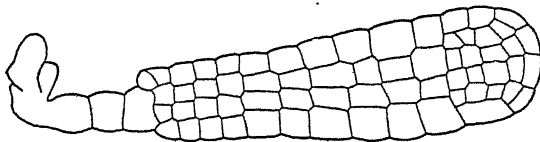


FIG. 36.
Embryo of *Aneura multifida*. (After Leitgeb.)

Aneura; so that the limits of the primary cells are more difficult to follow, as is also the number of segments which contribute to the capsule (Fig. 37). Both longitudinal and transverse sections of the sporogonium of *Porella* show a good deal of irregularity in arrangement of the cells, and it is clear from their comparison that the wall itself is not established by the first periclinals, as it is in *Radula* (Fig. 35). From such facts as these it follows that the cell-cleavages in the sporogonia of the Jungermanniales do not

necessarily connote early functional differentiation with any uniform degree of accuracy : in most of them, however, the segmentation is more regular than it is in *Porella*.

A high degree of interest attaches to the various modes of development of the capsule itself in the Jungermanniales. The inner contents are bounded by a protective wall, consisting commonly of two layers of cells : at maturity this splits as a rule into four sectors. Within it is the archesporium from which, after repeated cell-division, the sporogenic mass is formed. Many of the cells thus produced remain sterile as nutritive cells or elaters ; the remainder are spore-mother-cells. In certain cases it has been shown that the

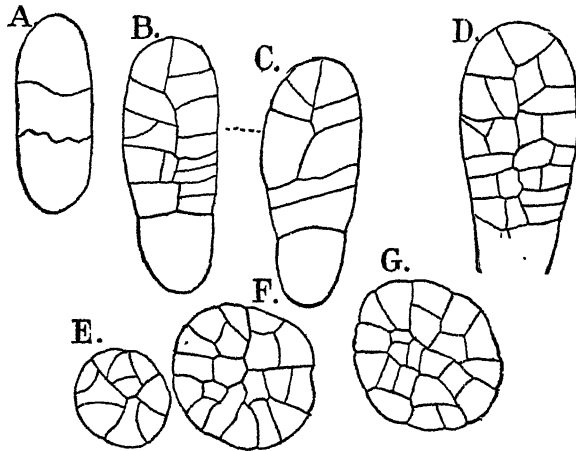


FIG. 37.

Porella Bolanderi. Development of the embryo. A-D, in longitudinal section. E-G, transverse sections. B and C are sections of the same embryo, and E, F, G are successive sections of a single embryo. $\times 525$. (After Campbell.)

elaters and sporogenous cells arise by division as sister-cells, in the same sense as in *Anthoceros* or *Notothylas*. In many of the Jungermanniales these are not arranged in any definite order, nor are the elaters attached either to the roof or floor of the cavity of the capsule. This is the state seen in *Porella*, also in *Radula* and *Jungermannia*. But in others the elaters may be attached to the wall of the capsule, or to a coherent mass of sterile tissue styled an elaterophore ; this may project from the distal or the basal end of the capsular cavity. Or, again, the elaters may be attached laterally to the capsular wall. This last is seen in *Cephalozia*, where the long elaters converge with their free ends inwards, while centrally there is a zone entirely free from them. When the ripe capsule splits, and the sectors become everted, the elaters radiate outwards, and their hygroscopic movements help in spore-dispersal.

In *Aneura* there is a distal elaterophore, to which some of the elaters are

attached; others are free, and radiate outward from it (Fig. 38). The development of the capsule has been followed. The wall consists of two layers of cells, while the massive archesporium lies within. The differentiation of this body is initiated early; in so young a sporogonium as that shown in Fig. 39 A there is a distinction, already marked by the protoplasmic contents, between a central group of more transparent cells and a peripheral band with denser protoplasm. The former gives rise only to the central part of the elaterophore, and later some of the inner products of the band shaded

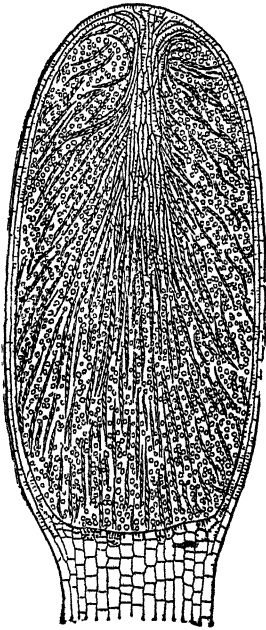


FIG. 38.

A. *Aneura pinguis*. Ripe capsule in longitudinal section. From the summit the elaterophore hangs into the spore-cavity, in which are many spores and elaters. Magnified. (After Goebel.)



FIG. 38, bis.

B. *Pellia calycina*. Sporogonium opened, and emptied, showing the valves of the wall recurved, and an elaterophore of many threads. (After Goebel.)

in (A) are also developed as sterile cells, while it is only the outer fringe that is finally fertile (B). This point is more clearly seen in the transverse section (C), which shows the relation of the sporogenous cells to the sterile tract. In *Pellia* the elaterophore is basally attached (Fig. 38 bis). Its development has been traced by Von Goebel (*l.c.*, Fig. 940), and corresponds in essentials (*mutatis mutandis*) with that in *Aneura*.

The sporogonium of *Frullania* differs from those above described by the fact that the elaters are attached at both ends till maturity, respectively to the outer wall and to the base of the capsule. The whole fertile region is here referable in origin to the four inner cells of the uppermost tier of the

early segmentation (Fig. 34, cells marked α). These cells divide with great regularity: the first divisions are horizontal, the upper layer is fertile, the lower sterile (Goebel, *l.c.*, p. 379); in the former the further cleavages are only longitudinal, and the result is a lens-shaped mass of about 200 cells arranged like a bundle of cigars. They differentiate also with great regularity into two types, sterile and fertile, which are disposed like the squares of a chess-board, as seen in transverse section. The sterile cells remain undivided, and relatively narrow; they number about 100, and each forms an elater with a single spiral band. The fertile cells distend and undergo repeated divisions transversely, before the final tetrad-division. The number of

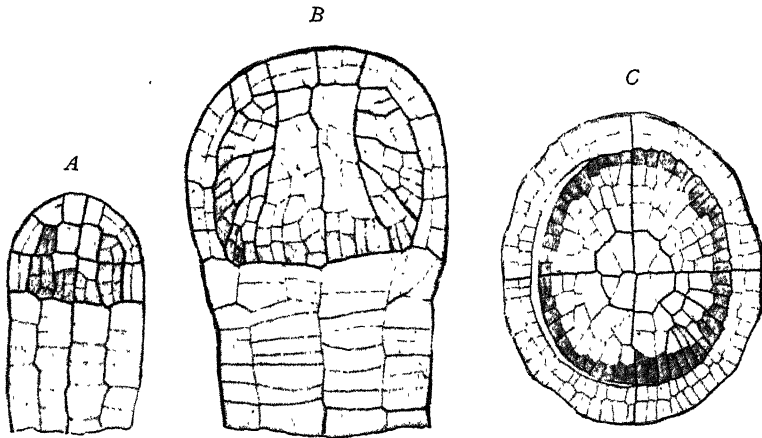


FIG. 39.

A, median section of young sporogonium of *Aneura ambrosioides*. The internal mass of cells of the sporogonial head ("archesporium") is already differentiated so as to indicate the sterile elaterophore, and the outer fertile region. *B*, the same, older: the indications of sterilisation have extended outwards, and it is only the peripheral fringe of cells (shaded) which will be sporogenous. *C*, transverse section of the same. $\times 150$.

spores may thus be several thousands, notwithstanding that these are all referable in origin to four cells. When ripe the sporogonium opens explosively from the apex, by crossed cleavages, and the four valves, having a thickening mechanism of the cell-walls, are reflexed. The elaters remain fixed at their upper end to the valves, and they then radiate outwards, and are effective in flicking away the spores to a considerable distance (see Cavers, *l.c.*, p. 120; also Von Goebel, *l.c.*, p. 888).

Freedom for the dehiscence of the sporogonium in such cases as this is gained by elongation of the seta; by this the calyptra is ruptured, and the capsule is raised above the margin of the perianth. In many Liverworts these two sheaths, together with an external involucre of bracts, constitute the protection of the sporogonium while young. But in certain types, described as the "marsupial" Acrogynae, an additional protection is developed which may involve the reduction of the perianth. The marsupial habit

appears to be a biological feature of homoplastic origin, and not characteristic of any one systematic group. The marsupium consists of a tubular development of the thallus which arises after fertilisation. It is seen in an extreme form in *Kantia*, as a pouch which grows at right angles to the creeping thallus ; it bores into the earth almost like a root, and bears rhizoids on its outer surface. The growth originates in a zone of tissue of the stem surrounding the perianth and involucre, forming a tube that is open upwards. The young sporogonium which develops within it is carried down into the soil by the growth of the marsupium, but as the fruit thus protected ripens the capsule emerges through the opening, being carried up by the elongating seta. The other sheaths, being superseded in their protective function, show various degrees of reduction.¹

Such features as those just described are accessory rather than fundamental, however high their value may be for systematic use. For purposes of morphological comparison the structure of the sporogonium itself provides more cogent material, and particularly the facts relating to the arche-sporium, and the proportion and distribution of the sterile and fertile cells which spring from it.

GENERAL COMPARISON OF THE LIVERWORTS

The preceding sketch presents some of the leading features of the Jungermanniales. It provides material not only for a rough seriation of members of this Order among themselves, but also for their comparison with other Liverworts. A key to the broad differences that are seen in them lies in the place taken by photosynthesis in a life-cycle that is similar for them all, and in the methods adopted to make this effective in relation to increase in size and in propagative capacity. It has been seen how in the Anthocerotales both the haplophase and the diplophase carry on photosynthesis, and are constructed accordingly. But in the Marchantiales and Jungermanniales only the haplophase is photosynthetic, and the sporogonium is physiologically dependent upon it. This fundamental fact probably helps to account for the relative constancy of general plan of the sporogonium in both of these Orders. Its elaboration is internal rather than external. The end served is to make the best use of the material indirectly acquired from the gametophyte, in maturing and disseminating the largest possible number of spores. This makes special demands upon the photosynthetic structure of the sexual phase. The response to this demand by the more plastic gametophyte has been divergent in the two Orders upon which it has specially fallen. The difference in their method characterises respectively the Marchantiales and the Jungermanniales ; the former have adopted *internal ventilation* of a thalloid expanse as a means of maintaining a due proportion of presentation-

¹ For further details see Von Goebel, *l.c.*, pp. 858-869, and Figs. 914-915.

surface as the size increases, while the latter have secured the same end by means of the foliar habit, which gives increased complexity of form and added presentation-surface *externally*. The result is a broad distinction between the thalloid and the foliar habit, either of which would serve to meet the physiological demand.

There is, however, no need for the distinction in form to be absolute, if either would serve; nor up to a certain point is either modification of form actually necessary under certain circumstances of life. A flattened thallus would be efficient up to considerable size in moist and shaded surroundings, as is seen in *Pellia*. Such a simple thalloid state might be primitive, or have been the result of reduction from one or other of the more elaborate forms. Thus the thallus of *Dumortiera*, or *Monoselenium*, or of *Euriccia* may be held to have resulted from hygrophytic degradation of a thallus of the type of *Marchantia*. The question must, however, remain open whether or not a similar interpretation of the thalloid Anacrogynae is permissible; their condition may well have been primitively such as they now are. Nevertheless in those juvenile forms of Acrogynae presented by *Lejeunia* (Fig. 29), and *Protocephalozia* (Fig. 30), either a secondary simplification or a continuance of a juvenile state would suffice. This view is supported by the fact that their sexual organs are borne on leafy buds later produced, which suggest a reversion of the adult to a more complex and probably pre-existent state. Such manifestations as these in the leafy Jungermanniales are in accord with the high degree of foliar specialisation which some of them possess; their adaptability is indeed comparable with that of the parts of the sporophyte in Flowering Plants. The problem of seriation of the Liverworts according to the complexity of the gametophyte is thus not so direct as it might appear. Allowance for reduction from some more complex state must be made where the actual structure is simple, as well as for advance from a simpler state where the form actually observed is elaborate. The original source in point of descent may well have been in a type neither the simplest nor the most complex of those now living.

From the description of certain sporogonia of the Jungermanniales given above certain general features emerge; in particular the early definition of exoscopic polarity, the constant radial construction, the absence of apical and the presence of intercalary growth, especially in the seta; the absence of photosynthetic tissue, the varying limit downwards of the fertile region, and, finally, the individual relation of the sporogenous to the sterile cells. The facts seem to suggest an internal solid core of fertile tissue as fundamental; but within this individual cells or tracts of cells have been sterilised, that is, diverted from their propagative function. The various types of capsule present various ways in which this sterilisation of potentially fertile tissue has advanced. One of these is by progressive limitation of the fertile tract from below; another is by distributed sterilisation of individual cells; a third is

by substitution of a sterile central core (the elatrophore), the fertile residuum being thus partially decentralised. But there is no evidence of a continuous or of a pre-existent columella. There can be little doubt that sterilisation has been a progressive feature in these sporogonia. The facts observed in those of *Frullania* are particularly cogent. Here the limitation of the fertile tissue from below is specially marked; in place of three tiers of segments being fertile, as for instance in *Radula*, only half of one tier produces spores; of the disc of cells which are recognised as the archesporium (Fig. 34, x, x), only the lower half that results from transverse fission is actually fertile; and of this again only one half of the cells are actually sporogenous, the rest forming sterile elaters. The whole structure of the capsule of *Frullania* is in other respects very highly organised, and this is so in a Liverwort which in its gametophyte presents a highly adaptive leaf-structure, with pitchers. The sporogenous tissue in this advanced type appears thus to have been whittled away by successive steps of sterilisation. Extending this conception of sterilisation so as to explain the origin of all the sterile tissues of the diplophase is a different matter, involving very wide comparisons. For the moment it must suffice to conclude that there is reasonable evidence of progressive sterilisation of fertile cells having taken place within the Jungermanniales.

The general conclusion which may be drawn from the study of the Jungermanniales is that they represent a very successful evolutionary line. This is witnessed by the numerous genera and species, by their wide geographical spread, and by their successful capture of the damp habitats that suit them. But their success is very limited as regards stature, particularly that of the gametophyte; though the erect position of the capsule, so important for the dissemination of the spores, is in striking contrast to its creeping habit. Up to a point both phases have been highly adaptive. In the gametophyte this is most marked in the leaf-development, which reaches its climax in certain epiphytic and rupicolous forms. But it is also marked in the nursing methods adopted by the marsupial types, which are dwellers on the soil. A third line of specialisation is in the internal differentiation of the capsule, in which advancing sterilisation is connected with an elaborate mechanism for distribution of the spores. In any or all of these lines the most complex may be held as the most advanced, but the evolutionary aspect of this is strengthened when any two of the lines of adaptation are marked in the same individual life. Since the marsupial habit is characteristic of earth-dwellers, and the higher foliar development of epiphytes, it is not probable that these would coincide. On the other hand, the fact that such a type as *Frullania* with its highly specialised pitcher-leaves has also a highly specialised capsule, with signs of advanced sterilisation as a feature in its development, points it out as one of the most highly organised types of the Order.

Taken as a whole the Jungermanniales appear as a blind evolutionary sequence, which dates back at least to Upper Carboniferous Time (Walton, *Ann. of Bot.*, xxxix., p. 563; xlii., p. 707). But they do not appear to have given rise to any further development beyond what is seen in them to-day. The success they as well as the Marchantiales have gained in their high variety of detail may be attributed to their high adaptability. What has checked the further advance of these Liverworts has probably been that, *while they adopted with limited success either internal ventilation or foliar elaboration, they never associated these in the same organism, as the higher land plants have done.* The vegetative development remaining thus stunted there was no demand for a specialised conducting system, and the gametophyte remained small. On the other hand, the sporogonium never departed from the simple unbranched state. Whether or not it may have once been photosynthetic, as in the Anthocerotales, it is not so now: and being thus physiologically dependent the sporophyte has been necessarily checked by the same restrictions as have governed the development of the gametophyte.

In conclusion, fungal infection in the Marchantiales and Jungermanniales remains to be considered. It has long been known that mycelial filaments occur regularly in the tissues of many Liverworts, and the question of a symbiotic relation with reciprocal advantage has been raised. Němec recorded the occurrence of fungal hyphae in the rhizoids of various Liverworts, and noted especially in *Kantia* how the nuclei of the invaded cells placed themselves in close proximity to them. The infection extended also to the thallus itself, and even occasionally to the sporogonium. But for Liverworts at large records by various observers have been contradictory. In explanation of this evidence has been found of immunity and of effective control by the host. In particular, it has been shown that in the thallus of *Pellia* a zone of immunity to infection, marked by destruction of the invading hyphae, surrounds the living archegonia and antheridia, and also the young developing sporophytes up to their maturity, though later the mycelium might invade the surrounding tissue. Such observations tend to clear up the confusion of records based upon isolated sections rather than on observation of the whole plant. On the other hand it has been held by some observers that the infection was limited to the gametophyte; as a matter of fact this is not so; but Cavers, who recorded several instances of penetration of the sporogonium, held that the relation in the sporophyte was simply that of parasitism. On the whole question it appears that at least in the gametophyte the relation, where it is present, is of similar biological nature to that of mycorrhiza elsewhere. Such facts and opinions, though not finally conclusive, bear a special interest in relation to the mycorrhizic state so well known in Pteridophytes, and particularly in the Psilophytales, Psilotales, and Lycopodiales.¹

¹ See Rayner, "*Mycorrhiza*," *New Phyt.*, Reprint No. 15, chap. ix., where the literature is fully quoted

CHAPTER IV

SPHAGNALES AND ANDREAEALES¹

THESE two Orders, though markedly different in habitat and external character, differ from most other Mosses in respect of certain important details of their development. Each Order comprises only a single genus, but the characters of each are so distinctive as to justify the ordinal rank which has been assigned to them. Further, those characters, particularly of the sex-organs and of the sporogonium, are such as to suggest in either case a position intermediate between the Liverworts and the other Mosses. Here they will be described separately, with particular reference to those features which possess special value in comparison.

SPHAGNALES

There are few genera of living plants which have taken possession of so large an area of the earth's surface as *Sphagnum*. The Bog Mosses are particularly widespread in northern circumpolar regions. There is no need here to describe in detail the general characters as seen in the adult state on any wet moor. Their success in capturing ground, and the large number of described species (336), distributed in all quarters of the globe, are a sufficient witness to the efficiency of their water-logged shoot. But in the association of living cells with the so-called "hyaline" dead cells in leaf and stem the genus does not stand alone. In the Leucobryaceae, though they are true Bryales, the leaves have a like structure; but this is clearly of homoplastic origin, since they differ from the Sphagnales in essential features. Moreover, the biological effect of that structure may not be the same, for the Bryales which show it are not always of water-logged habit (Von Goebel, *l.c.*, p. 964).

The germination of the spore of *Sphagnum* results in a juvenile stage of an unusual type. A short germinal filament widens into a flat expanse of

¹ *Selected Literature on Sphagnales and Andreaeales*: Berggren, *Andreaeaceae* Lund., 1868. Kühn, *Z. Entw. d. Andreaeaceen*, Leipzig, 1870. Haberlandt, "Beitr. zur Anat. u. Phys. d. Laubmoose," *Pringsh. Jahrb.*, 1886. Waldner, *Entw. d. Sporogon von Andreaea und Sphagnum*, Leipzig, 1887. Cavers, *New Phyt.*, Reprint No. 4, 1911, chaps. vi., vii., where the literature to that date is fully cited. Bryan, "Archegonium of *Sphagnum*," *Bot. Gaz.*, lix., 1915, p. 40. Campbell, *Mosses and Ferns*, 1918, chap. v., where the literature is fully cited. Ruhland, *Natürl. Pflanzenfam.*, 10 Bd., Leipzig, 1924, pp. 101-131. Von Goebel, *Organographie*, iii. Aufl., 1930, *passim*. Verdoorn, *Manual of Bryology*, 1932, *passim*.

variable structure, but only one layer of cells in thickness. By growth and segmentation of any one of its marginal cells a bud may be initiated, giving rise to a leafy shoot (Fig. 40). The structure of the first leaves is simple, but the fourth or fifth leaf begins to show the characteristic cell-differentiation

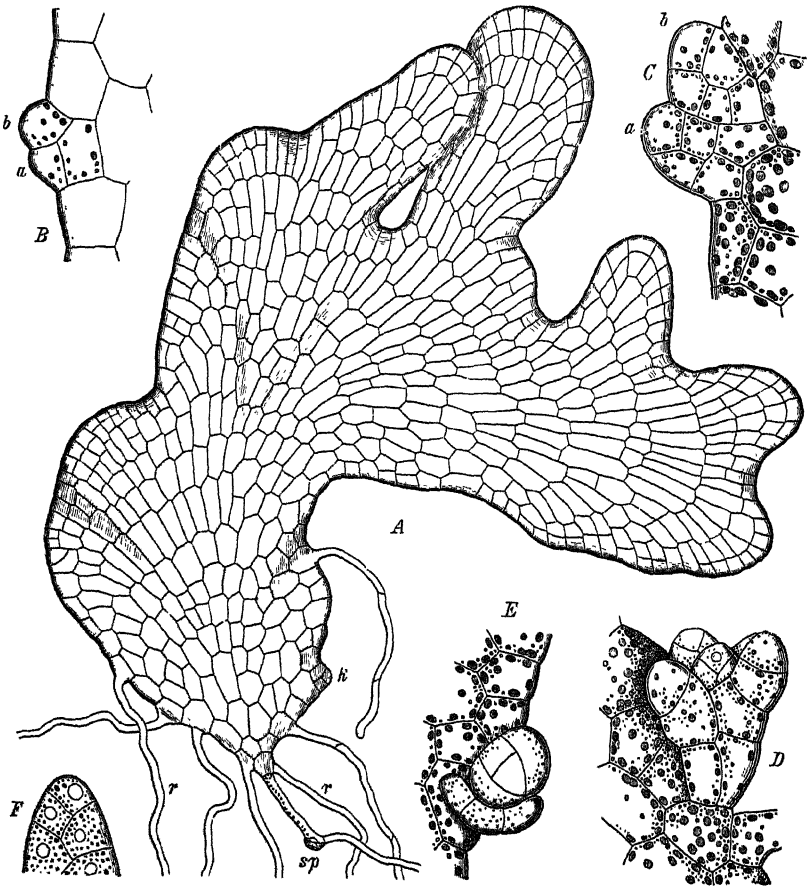


FIG. 40.

Protonema of *Sphagnum cymbifolium*, Ehrh. A thallus of medium size, many months old; *sp*, wall of spore; *r*, *r*, rhizoids; *k*, first stage of a shoot. B, marginal bud; *b*, acroscopic leaf-forming segments; *a*, basiscopic segment which forms the stem-apex. C, bud further advanced. D, young bud with primordial leaves. E, apical view of bud. F, apex of bud more advanced than D. (After C. Muller, from E. and P., *Nat. Pflanzenam.*)

of the adult. From such buds arise the ordinary plants, furnished with rhizoids below, and possessing the well-known complicated branching. As the main axis elongates indefinitely it is separated from its base by progressive rotting, and continues without any rhizoid-attachment. This is the condition usually seen in old moorland plants of *Sphagnum*.

However interesting the vegetative structure of *Sphagnum* may be as a special case of biological adjustment in relation to water, a greater comparative interest lies in the details of the sexual organs, which are remarkably uniform throughout the genus. They arise in the autumn upon special branches, either on the same or on different plants. The male branches appear first, and are recognisable as small catkins, capable of proliferation after the antheridia ripen. These are associated with leaves resembling foliage leaves, but closely overlapping in straight or spiral rows. Each antheridium is seated at the margin of a leaf-insertion, thus taking the place where a vegetative branch may normally arise. It springs from a single cell, which after several transverse segmentations passes on to alternating

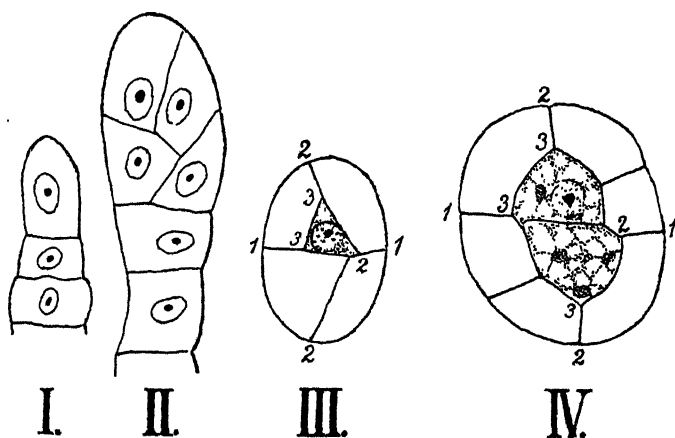


FIG. 41.

Sphagnum acutifolium. Development of the antheridium after Mellin. I. and II., young stages in longitudinal section. III. and IV., in transverse section. It is seen that no quadrant-division occurs, but the walls, 2, 2, are oblique. (From Von Goebel.)

cleavages of a two-sided apical cell. The further segmentations, and the cutting out of the fertile cells from those of the sterile wall, follow the lines of most Jungermanniaceae and Mosses, and as in them the antheridium ruptures distally (Fig. 41).

The archegonia of *Sphagnum* are borne on green bud-like branches. As in the acrogynous Liverworts the apical cell may actually become a primordium, but its latest segments also form secondary archegonia. There is some irregularity in the early segmentations, but as soon as the primordium advances its segments follow in a manner usual for Bryophytes. In the terminal cell three oblique walls cut off three peripheral segments surrounding the primary axial cell (14), which on transverse division gives rise to a cover-cell and a central cell (19). The cover-cell cuts off no basal segments, but forms a rosette of cells eight or more in number closing the apex of the archegonium. The central cell forms a primary canal-cell and a primary

ventral cell; the latter giving rise finally to the ventral canal-cell and the ovum (20). Meanwhile there is intercalary growth of the wall-cells of the archegonium, while those of the slightly enlarged venter divide periclinally to form two layers (40). It thus appears that the development is essentially of the Hepatic type, but that there are some minor differences which point in the direction of the Mosses (Fig. 42).

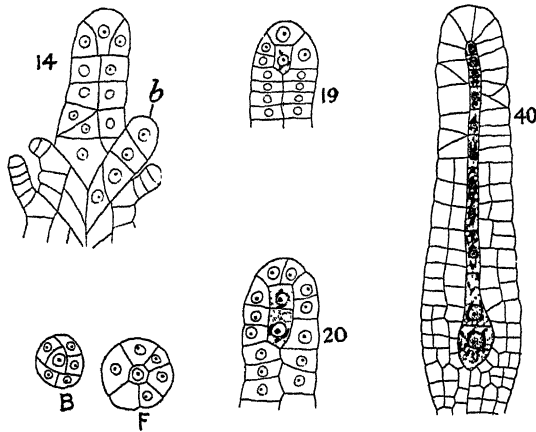


FIG. 42.

Archegonium of *Sphagnum*; stages of development. (After Bryan.) 14, stalk bearing a primary archegonium, with its primary axial cell already defined. A secondary archegonium (b) is cut in median section, showing two transverse cleavages in its stalk. 19, the primary axial cell divided into the cover-cell and central-cell. 20, the cover-cell has divided to form the distal rosette; the central-cell has also divided to form the primary neck-cell, and the primary ventral cell. 40, an archegonium approaching maturity, showing nine neck canal-cells, the ventral canal-cell, and the ovum. B, F, transverse sections through young archegonia, showing the three oblique segmentations which define the primary axial cell within the archegonial wall.

These details have been given explicitly because their comparative effect is to show how the sex-organs of *Sphagnum* take an intermediate place, even in details of segmentation, between the Liverworts and the Mosses. We have in this genus the remarkable condition that the development of the antheridium is after the manner of the Mosses, but that of the archegonium follows the Liverwort type (Goebel, *l.c.*, p. 659). Fertilisation takes place in early spring, and the mature fruits are found in the summer. Each is borne on a pseudopodium formed by intercalary growth of the gametophyte, and the button-shaped base of the seta is inserted into its distal end. This and the erect capsule itself are enclosed for a time in the enlarged venter of the archegonium, and its neck may be seen till ripeness is approached, projecting immediately above the centre of the operculum (Fig. 43 H). But it peels off at last, so that the capsule is exposed, though the seta with its button-shaped base is still ensheathed.

The capsule as it approaches maturity is nearly spherical, with a central columella overarched by the dome-shaped spore-sac. This is protected by a

wall some five layers of cells in thickness, the outermost being developed as an epidermis, which bears many rudimentary stomata. Each of these consists

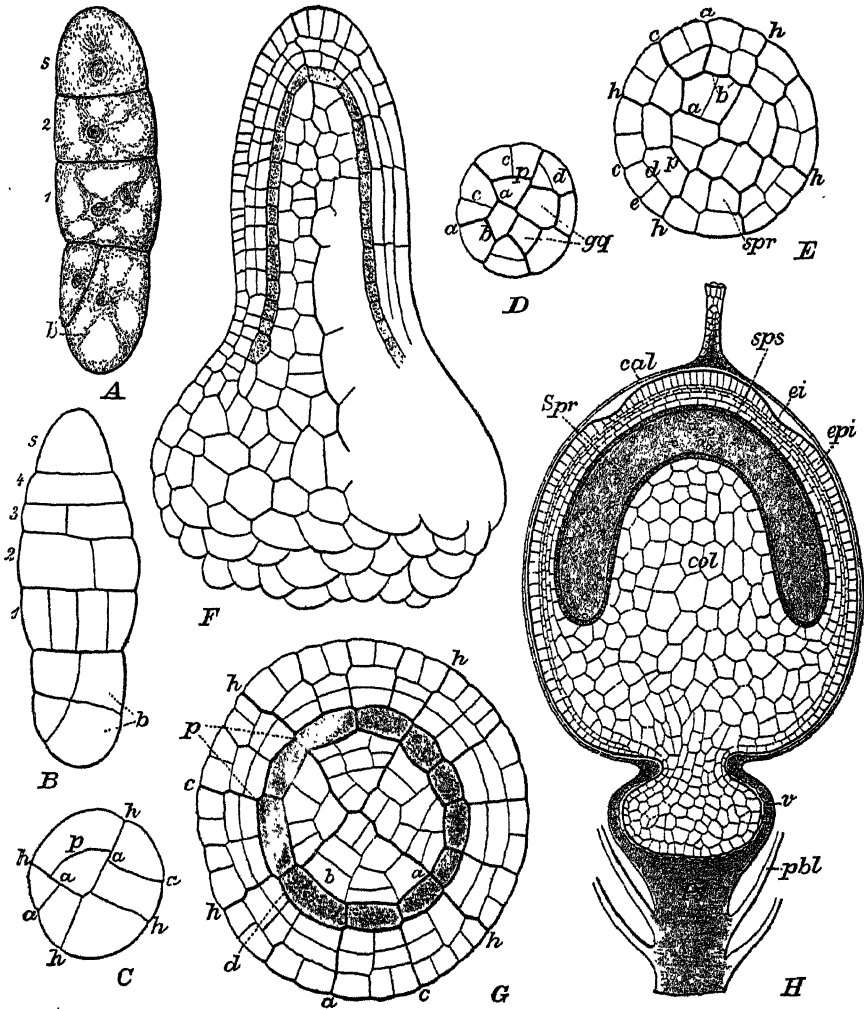


FIG. 43.

Development of sporogonium of *Sphagnum acutifolium*, Ehrh. A=embryo with four tiers; s=apical cell; b=basal cell with oblique division. B=embryo with five tiers. C=optical section of the same embryo; one quadrant is still undivided; a=anticlinal; p=periclinal walls; h=principal walls. D=transverse section of the lower part of an embryo. E=a rather older stage; spr=spore-forming layer. F=median longitudinal section of a sporogonium showing the bell-shaped sporogenous layer, and the wall covering it externally. G=transverse section of a sporogonium of similar age; lettering as in E. H=median longitudinal section, though a half-ripe sporogonium; cal=calyptra; sps=spore-cavity, in which the spore-mother-cells are isolated; sps=spore-sac; epi=epidermis; v=furrow in wall where the operculum will separate; ps=pseudopodium; v=vaginula; pbl=perichaetial leaves; col=columella. (After Waldner, from Engler and Prantl.)

of a pair of sister-cells derived by fission from a single mother-cell; but the partition-wall does not split so as to form an actual pore, nor are inter-

cellular spaces present in the tissue of the wall. As in certain other Bryophytes their presence appears to point to a former rather than to a present functional state. The dehiscence of the capsule is by means of a circular slit, which liberates a disc-shaped operculum, the horizontal line of cleavage being structurally defined by the less stature and strength of the cells of the wall (Fig. 43 H). The actual rupture, which is explosive and even audible, has been shown to result from drying up of the columella, which is replaced by gas. This again is compressed by contraction of the wall of the capsule on drying, till the pressure is suddenly relieved by rupture along the slit of dehiscence, and the spores are forcibly blown out.

Not only is the mature structure of the sporogonium of *Sphagnum* interesting for comparison with that of other Bryophytes, but also its development. Alone among the Mosses, with which it is rightly placed, its embryo segments by successive transverse walls, like the Liverworts (Fig. 43 A, B). There is no continued apical growth, the further enlargement after the first segmentations being intercalary in the segments already laid down. Of these the upper three or four go to form the capsule, the rest form the short seta and the foot. In the upper region each segment divides into quarters, which again divide so as to form in each transverse section a central group of four cells (endothecium), and a peripheral series (amphithecium) (Fig. 43 C, D, E). The former give rise to the columella alone, which is here a bulky mass of tissue with a rounded apex (F, H). The peripheral series of cells, or amphithecium, divides periclinally to give off internally the single layer of the archesporium; this appears as a continuous dome closely investing the columella. The external product of the amphithecium forms the many-layered capsular wall (F, G, H). The dome-shaped archesporial layer divides later into four layers, and every cell undergoes the tetrad-division to form spores. Meanwhile the foot enlarges as an haustorium, and the whole is borne upwards on a more or less elongated pseudopodium developed from the parent gametophyte (H).

The points of resemblance of the sporogonium of *Sphagnum* when young to that of *Anthoceros* appear in its segmentation, and in the absence of apical growth: also in the origin of the columella from the whole of the endothecium, and of the archesporium from the primary capsular wall outside it. Differences exist, however, in the mode of dehiscence, and in the fact that in *Sphagnum* there is no ventilated photosynthetic system, though this is well-developed in *Anthoceros*. Already in 1886 Haberlandt had demonstrated functionless stomata in large numbers, without pores or intercellular spaces below them, on the capsules of *Sphagnum*. From such facts he concluded not only that the ancestors of the present Bog Mosses had normal functional stomata on their capsules, but also that those of their ancestors possessed a relatively well-developed assimilatory system. The same argument may be extended also to the gametophyte of *Anthoceros*, and to the

capsules of certain Mosses. The whole question of these functionless stomata, and their bearing on the morphology of the Bryophyta, will be taken up at the conclusion of the Chapters relating to these plants (p. 104).

Sphagnum has always been ranked as a Moss on general grounds of habit. But now not only does the evidence from the sexual organs point to an intermediate position between the Mosses and Liverworts, but also the primary segmentation and the absence of apical growth in the sporogonium, and the amphithecial origin and complete dome-shape of the archesporium, are all features which point rather to the Anthocerotales than to the true Mosses. Such equivocal comparisons give a special comparative interest to *Sphagnum*. They serve to link together the two large groups of the Bryophyta, and in particular they suggest broad comparisons in respect of their sporogonia. It has been seen that in the Anthocerotales, while the archesporium of *Anthoceros* is amphithecial in origin, in *Notothylas* the whole endothecium may be fertile. Thus within that natural alliance the functional distinction is not constant. This conclusion will have to be extended to the Mosses also; and speaking generally for the Bryophyta it will be necessary to envisage a general process of decentralisation of the fertile tract, sometimes with a greater or less prominence of a central sterile columella or sometimes with none at all. In such a process *Anthoceros* and *Sphagnum* illustrate a more complex state, with the archesporium of amphithecial origin. *Notothylas* and most Liverworts are examples of a simpler state, not decentralised; but in the majority of Mosses the origin of the archesporium takes a middle position in relation to the primary segmentation, for it springs from the outermost zone of the endothecium, the inner part of it forming a well-marked columella.

Lastly, the thalloid stage which precedes the leafy plant in *Sphagnum* (Fig. 40) has its interest in relation to such a juvenile stage as is seen in *Lejeunia* (Fig. 29) and some other Liverworts. The formation of these broad expanses may be compared with those seen in certain other types which by their general characters are held as taking a relatively primitive place among the true Mosses, such as *Tetraphis* and *Diphyscium*. (Fig. 68).

ANDREAEALES

This Order is, like the Sphagnales, represented by a single genus, but it includes about 100 species of wide distribution. They are found chiefly in the colder regions, and often on rocky sites on mountains; they have a prevalent dark colour and a low creeping or densely tufted habit. The leafy plant is preceded by a juvenile stage of protean character. The germination of the spores is peculiar, in that a mass of cells is formed within the still-closed wall, and a number of these on its rupture grow out into filaments, some of which apply themselves closely to the substratum, branching freely; others

are erect (Fig. 44, 1-9). Where the protonema grows appressed to a rocky surface it widens out to a many-lobed and highly-branched expansion, thus providing a suitable means of establishing the plant on its chosen site (Fig. 44, 10). Buds may be formed at various points, which develop into

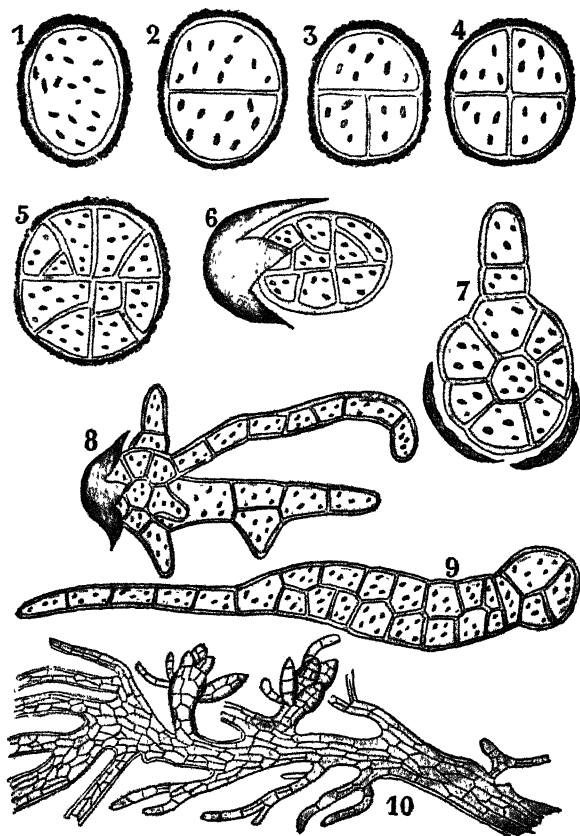


FIG. 44.

Germination of *Andreaea petrophila*, after Kuhn and Berggren. 1-6, formation of cellular body within the spore; 7-9, its further germination. 10, older protonema. (From Von Goebel.)

leafy plants similar in general features to those of the smaller Bryales. Thus the protonema shows a high degree of adaptability (Von Goebel, *l.c.*, p. 924).

The leafy plant of *Andreaea* is similar in essentials to that of the Bryales. The sexual organs conform to the type of the Mosses in presenting in either case apical segmentation. In the antheridium, which is long-stalked, the distal cell is two-sided, and the body of the antheridium is built up from two rows of its segments. The first archegonium may be formed directly from the apical cell of a branch, as in the Acrogynous Liverworts. After the

initiation of the short stalk the primordium cuts off the usual three lateral segments, leaving centrally a cell shaped as a truncated three-sided pyramid. The outer cell formed by its first periclinal division becomes the initial cell for the neck, and for the series of canal-cells; the inner forms the ventral canal-cell and the ovum. Thus the archegonium follows the well-known segmentation of the Mosses (Fig. 59). This is important for comparison with *Sphagnum*, where, though the antheridium conforms to the type of the Bryales, the archegonium points in its segmentation rather to the Hepatics. This divergence is all the more interesting since the two families treated in this Chapter conform in certain peculiar features of their sporogonia. In *Andreaea*, as in *Sphagnum*, the seta is short, and the whole is borne up on an elongated pseudopodium: but the venter of the archegonium is ruptured as the capsule enlarges, leaving a basal vaginula, while the distal calyptra is carried up on its tip (Fig. 45). At ripeness the capsule opens by four longitudinal slits: these do not extend to the apex, as is usual in Liverworts; the ends of the four valves remain united, and there is no peristome (Fig. 46). When dry the slits gape widely, but when moist they are closed.

The development of the capsule of *Andreaea* presents features of special interest for comparison. The segmentation of the zygote corresponds to that of other Mosses rather than to that of the Hepatics or of *Sphagnum*; for after the appearance of the transverse basal wall the cleavages are oblique, a two-sided initial cell being present (Fig. 47, A-D). But the number of such segmentations is limited to about a dozen. The segments

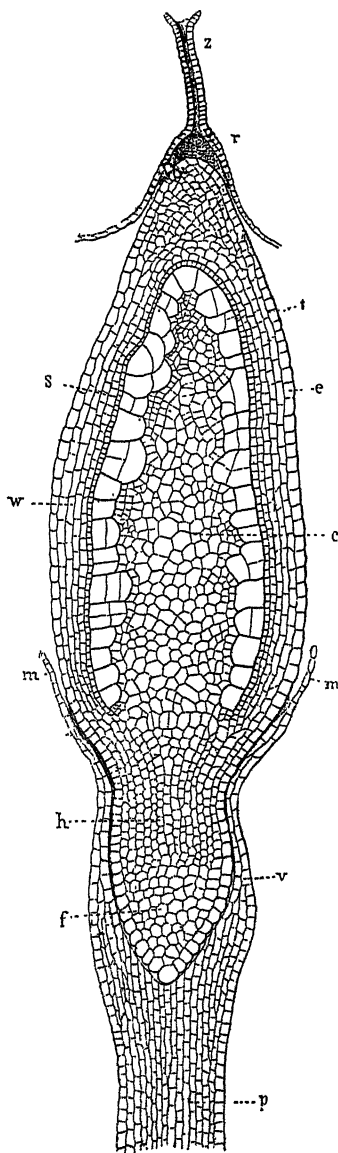


FIG. 45.

Median longitudinal section of sporogonium of *Andreaea rupestris*, at the time of division of the archesporium. *p*=pseudopodium; *f*=foot; *v*=vaginula; *n*=neck; *c*=columella; *w*=wall of sporogonium; *e*=epidermis; *s*=spore-sac; *t*=archesporial cells dividing; *r*=calyptra; *z*=neck of archegonium. (After Kühn.) $\times 80$.

undergo further sub-divisions to constitute an endothecium of four cells in transverse section, and a many-celled amphithecium (Fig. 47, G). The hypobasal half of the zygote has meanwhile undergone irregular divisions. The two lowermost segments of the epibasal region remain sterile, and these, together with the hypobasal half of the zygote, constitute the seta and the foot. The differentiation of the archesporium begins in the lower part of the epibasal region, as is shown in Waldner's drawing (Fig. 47, E); later it is completed upwards, forming a dome (Fig. 45), as it is in

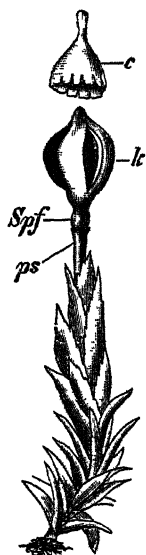


FIG. 46.

Andreaea petrophila;
Plant bearing sporogonium. *ps*, pseudopodium; *Spf*, foot.
k, capsule; *c*, calyptra.
× 12. (After Strasburger.)

Sphagnum or in *Anthoceros*. If it stopped at the earlier stage it would be of the type usual for the Bryales (Von Goebel, *l.c.*, p. 670, Fig. 652); for the archesporium is here derived from the endothecium, the peripheral cells of which after repeated divisions give rise to spore-mother-cells, while the innermost form the sterile columella (Fig. 47, E, J, K). The internal limit between the archesporium and the columella is in *Andreaea* very irregular, as it is also in certain Cleistocarpic Mosses.

It thus appears that though *Sphagnum* and *Andreaea* have certain characters of the sexual organs and of the sporogonium in common, their segmentation does not follow any uniform scheme, and the comparisons with other Bryophyta likewise follow irregular lines. For instance, the archegonium of *Sphagnum* segments as in the Hepatics, that of *Andreaea* follows the plan of the Mosses. Further, while the archesporium of *Sphagnum* originates from the amphithecium as it does in *Anthoceros*, that of *Andreaea* arises from the outermost cells of the endothecium, as in ordinary Mosses. Nevertheless, the dehiscence of the capsule in *Sphagnum* is transverse,

liberating an operculum, as is usual in Mosses; that of *Andreaea* is by four longitudinal slits, as in many Liverworts. In both genera the leafy plant compares with the Mosses rather than with the Liverworts; but in both there are flattened thalloid expansions that follow on germination, and recall the thalloid gametophytes of Liverworts: similar developments do occur, however, also in certain relatively primitive members of the Bryales. The existence of such divergent comparisons will tend to confuse detailed questions of affinity rather than to resolve them. These genera appear to occupy each an intermediate but isolated place between Mosses and Liverworts; but their characters do not concentrate in either case so as to point to definite affinity with one another, nor yet with any single genus of either Class. Nevertheless, these comparisons and contrasts certainly have the cumulative

effect of drawing the two Classes of the Bryophytes together, and that will afford justification for treating the Bryophytes as a coherent whole, notwith-

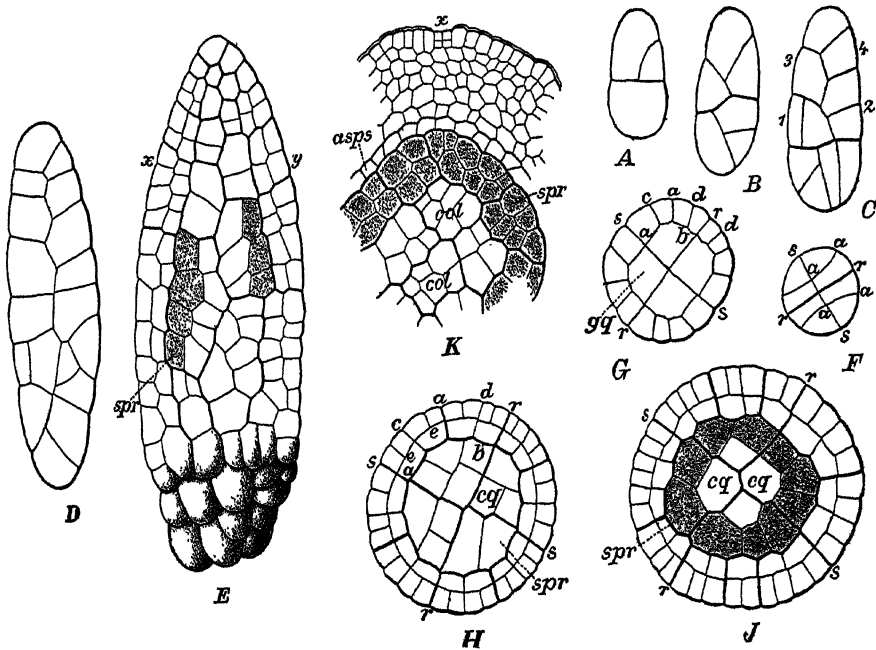


FIG. 47.

Development of sporogonium of *Andreaea*. A=young embryo of *A. crassinervia*, Broh. B=*A. petrophila*, Ehrh. C=of *A. crassinervia*, older. D=of *A. sp.*, older still. E=optical longitudinal section of *A. petrophila*; *spr*=archesporium. F=optical transverse section of a young embryo; *s*, *s*=segment-walls; *r*, *r*=radial walls; *a*, *a*=first divisions of the quadrants. G=older stage; *gq*=“grund-quadrat.” H=older stage with division to form archesporium. J=archesporium differentiated. K=archesporium divided into two layers; *osps*=outer spor-sac; *col*=columella. (After Waldner.) D after C. Muller-Berol. (From Engler and Prantl.)

standing the degree of divergence in detail which the constituent Orders of them individually present.

CHAPTER V

BRYALES¹

UNDER this heading the great majority of the Mosses are included. They form a natural group of organisms that are obviously related, notwithstanding the fact that their genera and species are very numerous, and their habitats diverse. Though many of them can endure drought, they are dependent upon a sufficient water supply during their periods of active growth, and particularly for their sexual propagation. Some of them are actually submerged (*Fontinalis*), many are swamp-growers; but others may occupy exposed situations, such as rocks, wall-tops, and roofs. Others again are epiphytic, particularly in the dripping forests of the tropics, or in woods as well as in the open on the misty hills of temperate regions. There is reason to believe that some at least behave as partial saprophytes.

The Bryales are never large; some of them are very minute. As extremes may be mentioned the male plants of *Buxbaumia*, which are hardly visible with the naked eye, while the stems of *Dawsonia* may grow to a height of about 50 centimetres. But many types are of creeping habit, and may extend over a larger area than their actual height would suggest. Often these Mosses are gregarious, forming dense cushions of rounded form, or covering considerable areas as a pure but miniature vegetation. This naturally follows from the production of buds freely upon the filamentous protonema, which is a constant predecessor of the leafy plant. Moreover, an evergrowing soil is acquired for each cushion by the capture of wind-borne dust between the closely ranged shoots. The leafy plant is very freely branched in many of the larger types, but the leaves themselves are simple and their size relatively small.

¹ *Selected Literature on Bryales*: Kienitz-Gerloff, "Sporogonia," *Bot. Zeit.*, 1878, p. 36. Haberlandt, "Beitr. z. Anat. u. Phys. d. Laubmoose," *Pringsh. Jahrb.*, 1886. Vaizey, "*Splachnum luteum*," *Ann. of Bot.*, 1890, p. 1. Cavers, *New Phyt.*, Reprint No. 4, 1911, "Bryales," chap. viii. Correns, *Unters. über die Vermehrung d. Laubmoose*, Jena, 1899. Tansley and Chick, "Cond. Tiss. of Bryophyta," *Ann. of Bot.*, 1890. Holferty, "Archegonium in *Mnium. undulatum*," *Bot. Gaz.*, xxxviii., 1904. Jongmans, *Brutkörper—bildende Laubmoose*, München, 1906. Dickson and Jameson, *Student's Handbook of British Mosses*, 1896. Haberlandt, *Physiol. Anat.*, Engl. edn., 1914, p. 299. Campbell, *Mosses and Ferns*, 3rd edn., 1918, chap. vi. Ruhland, *Natürl. Pflanzenfam.*, Bd. 10, 1924, p. 94. Brotherus, "Bryales," *Natürl. Pflanzenfam.*, Bd. 10, 11, 1924. Von Goebel, *Organographie*, iii. Aufl., 1928, *passim*. Verdoorn, *Manual of Bryology*, 1932, *passim*: but particularly Von Wettstein, chap. ix., "Genetik," with full citation of literature.

THE GAMETOPHYTE OF THE BRYALES

Starting from the spore shed from a capsule of some ordinary member of the Bryales, such as *Funaria*, the outer wall is ruptured, and filaments project which as they grow are partitioned into cells, and soon branch freely. Some of the branches are exposed at the surface of the moist soil; these have as a rule transverse septa, and they develop chlorophyll (Fig. 48). Others burrowing into the soil are colourless or have brown walls,

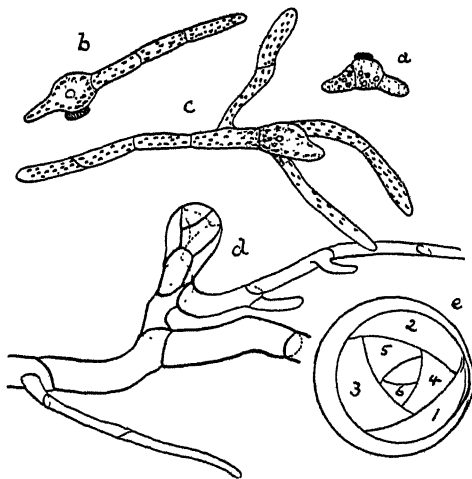


FIG. 48.

Protonema of Moss. *a*, *b*, *c*, germination of spores of *Funaria* to form protonema; *d*, formation of a bud laterally upon the protonema of *Barbula*; *e*, diagrammatic plan of the segmentations of *d*, as seen from above. (After H. Müller.)

and their septa are oblique: these serve as rhizoids, but they differ from the unicellular rhizoids of Liverworts in being partitioned; they are best held as underground protonemal filaments specialised for absorption. It was suggested by H. Müller that the obliquity of the successive septa corresponded to that of the cleavages in segmentation of an apical cell of the leafy shoot, and that consequently the rhizoids might be held to be an extended form of axis. But it is found that the orientation of the successive septa is not constant; moreover, the obliquity occurs as a rule only in the rhizoids. The oblique partitioning may more probably be recognised as an adaptive means of increase of surface in relation to the transit of water and of solutes from cell to cell, which is the chief office of the rhizoids (Von Goebel, *l.c.*, p. 915).

The formation of the leafy Moss Plant is regularly preluded by this filamentous stage. Each plant arises as a pear-shaped bud which takes the place of a basal branch of the protonema. Oblique cleavages soon establish a distal initial cell, its form being usually that of a three-sided pyramid;

but their divergence is rather more than 120 degrees, as is shown in Fig. 48, *d*, *e*, and Fig. 49, II. Each segment gives rise to a leaf of the Moss Plant ; the result for most Mosses is that the arrangement of the leaves on the

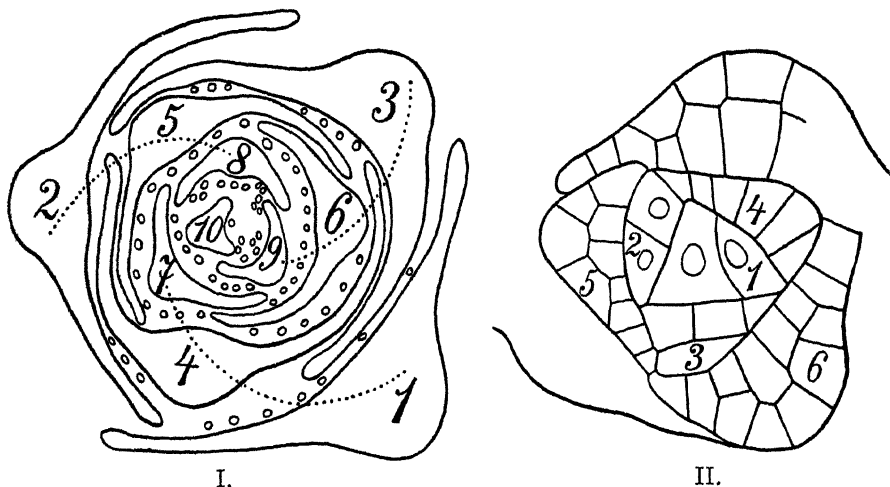


FIG. 49.

Catharinea undulata. I, Transverse section through a bud. The leaves are by "apical torsion" disposed in three curved series, as indicated by dotted lines. Between them are mucilage hairs. II, Transverse section through the apex, more highly magnified than in I. Six segments are numbered, but in reverse sequence to those in Fig. I. (After Von Goebel.)

elongating axis appears as a spiral more complicated than one of one-third divergence. In *Catharinea*, for instance, three parastichies are indicated by the dotted lines in Fig. 49, I, which include respectively the leaves numbered as 1, 4, 7, 10 ; 3, 6, 9 and 2, 5, 8. In other Mosses, however, the leaf-arrangement may be simpler, as, for instance, in *Fissidens*, where the apical cell is wedge-shaped and the leaves are arranged in two rows corresponding to the two sets of segments.

The vast majority of the Mosses have a three-sided pyramidal initial cell at the stem-tip. If all the sides of such a cell were equal, and if a leaf were produced by each, the divergence would be regularly one-third, and the leaves would be tristichous. This is so in *Fontinalis*, but it is rare. Usually each segment-wall is advanced in the anodic direction ; thus the want of symmetry is already seen in the apical cell before the leaves appear, and the leaf-symmetry is determined by the axis itself. In some Mosses a transition upwards from the regular one-third divergence to a degree of asymmetry may be followed in the individual shoot. This is readily demonstrated in those large Mosses which have leaf-trace-strands, such as *Dawsonia* (Von Goebel, *l.c.*, p. 298, Fig. 312). Successive transverse sections from below upwards have been found to present the traces in straight rows in the lower sections ; at a

higher point these show slight torsion, higher still a strong torsion. Such torsion is initiated by the segmentation of the apical cell itself, and so cannot be due to any hypothetical pressure of the leaves one upon another. There has been in fact a transition of the segmenting apex itself, before the individual leaves appear, from a symmetrical to an asymmetrical state. Thus the Mosses, with their strict relation of the leaves to the apical segmentation, yield the clearest possible evidence of the initiative of the growing point in leaf-arrangement. This bears upon the general question of leaf-arrangement for plants at large, for which the conclusion is stated by Von Goebel, as follows : " This much is proved, so far as we can see. The question relates to conditions of growth and symmetry that arise in the growing point. All

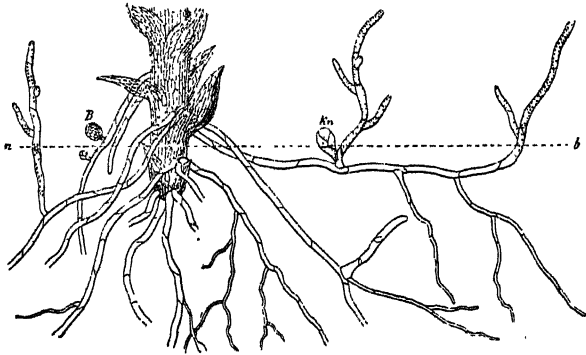


FIG. 50.

Lower part of stem of a Moss (*Barbula muralis*), with protonema. *a-b*, shows the soil-level. *B*, is a young gemma. *kn*, a bud that would grow into a new plant. (After H. Muller.)

theories as to leaf-position that allotted a passive rôle to the growing point were mistaken, however acute the reasoning that was brought to bear thereon" (*Organographie*, p. 300).

From a leafy bud thus originating from the protonema, and continuing its apical growth with or without branching, the ordinary Moss Plant arises ; additional protonemal filaments may push out from any cell at its base, from which again fresh buds may spring (Fig. 50). The whole vegetative system, built up from the filaments and leafy phases, is thus open to indefinite extension. There may be great variety in the balance of the protonema and the plant, but the protonemal phase is only vegetative ; as in the leafy Liverworts, the sex-organs appear only on the leafy plant, small though it may sometimes be. In ordinary ground-growing Mosses the balance in the adult is usually that seen in familiar examples such as *Funaria* or *Catharinea* (Fig. 51). After the formation of leafy buds the green protonema usually disappears, and only the rhizoids persist. But under special conditions the protonemal system may be continued indefinitely, without the formation of leafy plants at all, so long as these conditions are maintained. This was shown experimentally by Von Goebel in the case of *Philonotis fontana*, a

denizen of swamps. When grown on a slab of wood submerged in water heavily charged with sulphates and iron, the protonema assumed large dimensions, as a bulky cushion of filaments without leafy buds. An extension of the juvenile form was thus induced by external factors. It may also



FIG. 51.

Catharinea (atrichum) undulatum. The leafy gametophyte or Moss Plant bearing capsules or sporogonia, which represent the dependent sporophyte generation. (After Schimper.)

be encouraged by habitat ; for instance, in *Ephemeropsis tjibodensis*, a Malayan epiphyte growing on leaves of Monocotyledons, the protonema is not only extensive but specialised. It is dorsiventral, the main trunks creeping over the leaf-surface, while forked assimilating branches rise laterally from them, ending in long bristles. On the other hand, "hapteres"

closely applied to the leaf-surface fix the protonema. The fructifying leafy plant is, however, relatively small (Fig. 52). A like promotion of the filamentous stage and simplicity of the leafy plant appears normally in *Buxbaumia*, which will be described below. Such examples show that the balance of the two phases of the haploid generation is not fixed but adjustable.

The leaves of the Bryales are mostly thin in texture, and composed marginally of a single layer of cells, though often they are more massive, especially towards the base. The detail of their cell-structure varies greatly,

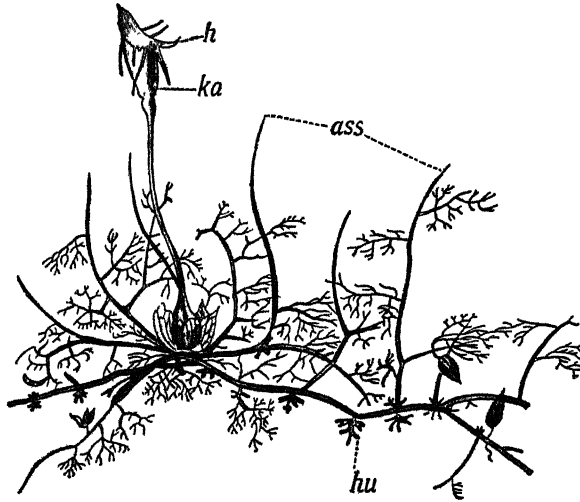


FIG. 52.

Ephemeroopsis tjibodensis. Protonema with a fruiting plant. *ka*, capsule; *h*, calyptra; *ass*, assimilating protonema; *hu*, hapteres. (After Fleischer, from Von Goebel.)

and material is thus provided for their specific classification. The cells for the most part contain chlorophyll. Those at the margin are commonly thick-walled, but destitute of cuticle; the tip is often extended into a stiff awn; sometimes it is long, as in *Barbula*. The smallest leaves have no distinct midrib, but in most of those of moderate size there is a median tract of elongated cells several layers in thickness. Where the size is largest this is traversed by a specific conducting strand, which may be traced downwards into the stem. Often such leaf-traces do not connect downwards to form a continuous conducting system for the shoot, but in the largest there may be a loose connection, as in *Polytrichum*, or *Dawsonia*.

The stem in many leafy Mosses of moderate size is traversed by an undifferentiated conducting cord of narrow and elongated cells. Its structure is not unlike that of a procambium strand of the higher plants. It is surrounded by thin-walled parenchyma, but towards the periphery of the stem the cell-walls become thick and resistant, forming a mechanical cylinder to which such stems owe their wiry texture. The larger Mosses show advanc-

ing degrees of differentiation of the central strand, till in such types as *Polytrichum* and *Dawsonia* a highly organised structure is presented, which is loosely linked up with the leaf-traces that approach its margin (Fig. 53). The inner stelar cylinder here consists of a compact mass of very thick-walled elongated living cells with oblique ends, containing starch. Scattered among these *stereids* are elements of about the same diameter, but without contents. They are sometimes solitary, sometimes in groups; they are thin-walled and are styled *hydroids*. In *Dawsonia* these are about

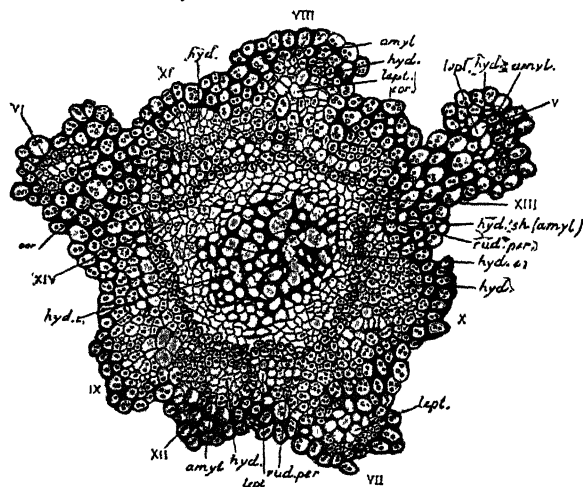


FIG. 53.

Transverse section of the central tissues of an aerial leafy stem of *Polytrichum commune*, showing entry of leaf-traces into the mantles of the central cylinder. The leaf-traces are numbered from without inwards. *amyl*, starchy parenchyma; *hydr.*, hydrom; *lept.*, leptom; *hyd.sh.*, hydrom-sheath; *rud.per.*, rudimentary pericycle. $\times 200$. (After Tansley and Chick.)

twenty times the length of the adjoining cells. Coloured fluids are found to pass rapidly up them, though not so quickly as is the fluid-transit in the wood of Seed Plants. The column of tissue thus constituted is continuous up towards the apex. It is surrounded by a sheath of living cells upon which the leaf-traces are inserted, and outside again is the cortex, becoming more and more indurated to the external surface.¹ Though not so highly organised as in the Seed Plants, it is seen that the stems of the larger Mosses possess a conducting system effective for plants of small size, and they are also mechanically strengthened at the periphery.

Biologically the relation of the leafy plant of the Bryales to the water supply is very intimately connected with their morphological structure. The complexity of the conducting system just described is roughly according to size. On the other hand, the development of the system of rhizoids is proportional to the demand; this is illustrated by the fact that if a sod of

¹ For recent observations on water conduction in Mosses, see E. J. Brown, *Ann. of Bot.*, 1931-1934.

Catharinea be cut out from the soil of a damp wood the plants shrivel, though those undisturbed do not. The external conditions remain the same for both, but the curtailed rhizoid-system of the sod does not suffice for so susceptible a Moss as *Catharinea*. *Polytrichum*, however, which possesses the well-known lamellar structure of its blade, is more resistant (Von Goebel, *l.c.*, p. 955). Such simple experiments serve to introduce the subject of the detailed structure of the Moss-leaf in its biological aspect. The form of the Moss-leaf is always simple. It is never so highly specialised in form for water-retention as it is in some Liverworts. But though pitchers are absent the leaves are not uncommonly folded so as to catch and retain water. The surface-contours are, however, often such as to bring a favourable result, even when the blade consists only of a single layer of cells. The simplest of such modifications take the form of small outgrowths, it may be by local thickening of the superficial wall only, or whole cells may form processes which constitute an effective capillary system when closely set together. Such surface developments as these appear mostly at the distal region of the blade, and are found in variously allied Mosses of exposed habit, rather than in those that are hygrophilous.

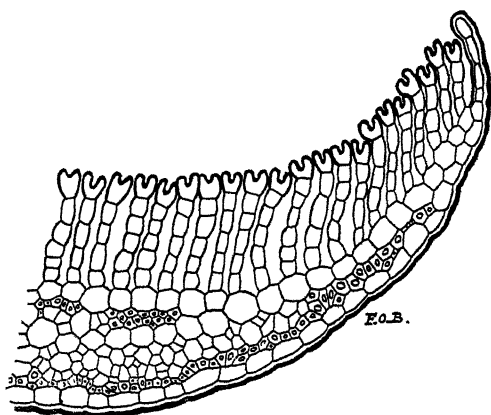


FIG. 54.
Half of a transverse section of a leaf of *Polytrichum commune*,
showing the longitudinal plates cut in section.

More complex outgrowths appear as cell-rows, or as continuous longitudinal plates, projecting from the upper surface of the blade, and often extending towards the extreme tip. Cell-rows closely packed and branched arise from the one-layered leaf of species of *Barbula*; they are attached to its upper surface, and form a complex sponge which is overlapped by the thin margins (Von Goebel, *l.c.*, p. 958). The best known of the surface-outgrowths are, however, those continuous plates of chlorophyll-containing cells which are found on the surface of the blade in *Catharinea*, *Polytrichum*, and *Dawsonia*. These are all relatively large Mosses, with elaborate leaves. The plates consist of thin-walled cells with plentiful chlorophyll. They are in fact the chief photosynthetic tissue of these plants. In *P. commune* the distal cells of each plate are enlarged so that the chlorophyll-cells abut upon an almost closed space (Fig. 54). The leaf flattens when moist and the plates separate, but it curls its margins upwards in drought, and the plates close. Not only may such a structure be

effective in catching and retaining external water, but also, in dry conditions, the access of atmospheric air is thus controlled in a manner analogous to that exercised by the stomata of Vascular Plants. This is only an analogy, for the surfaces of the lamellae are actually part of the outer surface of the leaf thrown into deep folds, while the intercellular channels originate internally. This mechanism in large Mosses has usually been described as a means of collecting and holding water, and no one would doubt that it is of use in that respect whenever external water is accessible. But the fact that in *Polytrichum*, where the lamellae are best developed, the tissues of the lamina itself are chiefly mechanical or serve for conduction, indicates that the green lamellae are the main photosynthetic tract; they serve alternatively for assimilation and for water-retention according to the conditions, and for both of these functions the structure as described would bring added efficiency.

Here also the existence of "paraphylls" may be mentioned. These are delicate outgrowths of chlorophyll-containing tissue which branch so as to form a capillary felt capable of holding water like a sponge. They are seen in rich development in *Hylocomium splendens*; this Moss lives under conditions not unlike those of the Liverwort *Trichocolea*, in which a similar structure is found. In origin, however, the paraphylls differ from leaves in that they vary in number and position, and are intercalated between the normal leaves, or they may even arise from their bases. In *Thuidium* they resemble in structure those branched protonemal filaments that spring from the surface of the stem in some other Mosses. The existence of empty cells with perforated walls has already been mentioned in *Sphagnum* (see p. 59). Various genera of the Bryales, and in particular *Leucobryum*, have a like habit useful in storing and retaining water. It thus appears that an adequate water supply in Mosses is maintained by various structural means, which all tend to secure vitality.

This brief general sketch may serve to illustrate how in the Bryales we see the gametophyte of Land Plants in its highest development. The analogies with the diploid phase of Vascular Plants are striking, but they are to be held as analogies only; they show in the most marked way how far homoplastic development may reach in securing ends similar physiologically to those served by the more elaborate mechanism of the Vascular Sporophyte. Two special features possessed by the Bryales help in accounting for their wide spread, and for their tight grip upon sites apparently unpromising. One is their elastic relation to water, the other is the exceptional profusion of their methods of vegetative propagation. The absence of cuticle accounts in some degree structurally for the ready absorption of liquid water wherever it is available at their surfaces; but also the physical qualities of the thickened cell-walls, particularly at the margins and tips of the leaves, is believed to have importance in the condensation of water-vapour from an over-charged atmosphere. With these structural features goes also a special power of

resistance to drought, and of maintenance of vitality in a state of physiological arrest.

Passing on to the methods of vegetative propagation of the Bryales it will not be necessary to describe more than a few examples. Probably no class of plants can show greater diversity in detail; but in principle the methods are all alike in this, that a preliminary protonemal stage heralds the formation of each new leafy plant. A filament may arise from any undamaged cell, either of the plant itself or of the protonema. If a sod on which Mosses are growing be inverted and kept moist, protonema and ultimately a new crop of Moss Plants will spring from the rhizoids already there. If leaves or stems be chopped up any undamaged cell may grow out under favourable conditions into protonema, giving rise to a new crop. But, besides this, in many Mosses certain parts are so developed during normal life that they are readily detached as gemmae, which may start new colonies in fresh stations. The protonema itself may break into short detachable lengths, as in *Funaria*, or gemmae may be formed upon it, as in *Barbula* (Fig. 50, B); or large numbers of gemmae may be formed on the surface of the leaves, as in *Grimmia*; or whole leaves may be slightly modified for the purpose, stored with nourishment, and break away from a narrowed brittle base, as in *Aulacomnion palustre* (Fig. 55). Germinated on moist soil any cell may produce protonema. Frequently, however, more highly specialised gemmae may be formed; for instance, those of *Tetraphis*, which are long-stalked and lens-shaped; they are borne in a distal cup formed of overlapping leaves that protect them while young (Fig. 56, A). Easily displaced, and falling on moist soil, any cell may produce a filament, and widen out into the broad expanse which is characteristic of this Moss. Near to its base a young moss plant is seen in Fig. 56, B. For further details references should be made to special treatises.

The haploid phase of the Bryales is thus seen to vary within wide limits both of structure and of vegetative propagation. The sexual organs are, however, much more constant in their characters, and in their development. Both antheridia and archegonia project freely from the surface of the plant, and are never sunken. They are sometimes borne on the end of the main axis (acrocarpic), sometimes on short lateral branches (pleurocarpic), a difference which has been held as a guide in classification, though now it has been discarded by most systematists. The sexual organs are often protected by specially developed perichaetial leaves, the end of the shoot taking an



FIG. 55.
Leaf-gemmae of *Aulacomnion palustre*. The drawing shows the scars where some of the gemmae have been shed.

almost flower-like appearance, as in *Polytrichum* and *Mnium*. In some Mosses the antheridia and archegonia are grouped together, as in *Meesia* (Fig. 57), while associated with them are numerous paraphyses (*p*). But more frequently the sex-organs are borne separately, either on distinct

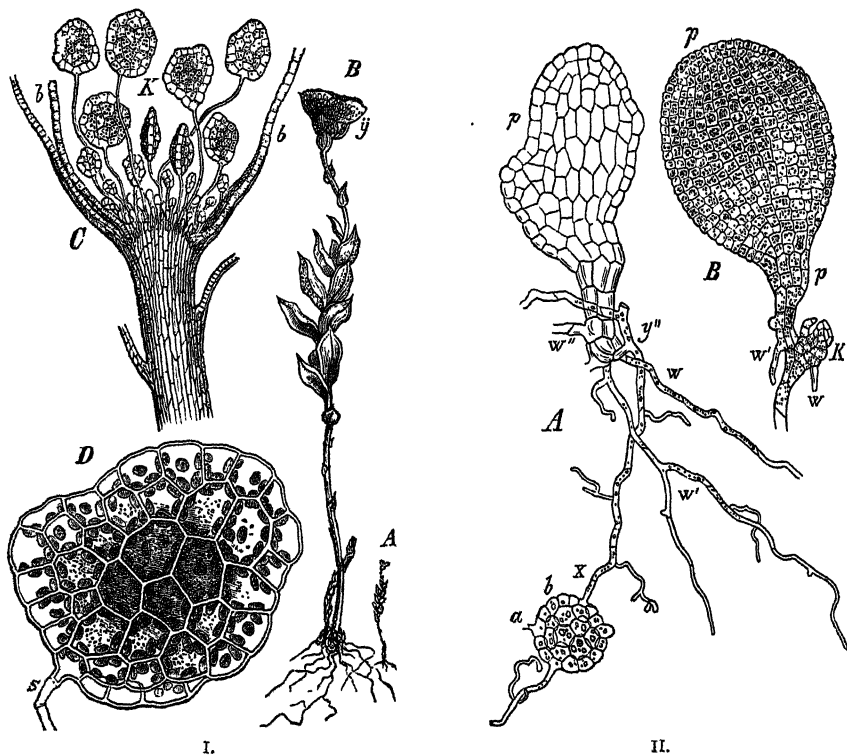


FIG. 56. *Tetraxis pellucida*.

I. A, a plant of natural size, forming gemmae. B, the same magnified: *y*, the cup in which the gemmae are borne. C, longitudinal section through the summit of B; *b*, the leaves which form the cup; *k*, the gemmae in various stages of development: the older gemmae are torn from their stalks by the growth of the younger, and thrust beyond the edge of the cup. D, a mature gemma, magnified 550 times, formed from one cell-layer at the margin, and several at the centre.

II. A, shows a gemma *b*, with the stalk broken off at *a*: a marginal cell of the gemma has grown out into the protonemal filament, *x*, *y'*, from which the expansion *p* has been formed as a lateral shoot: and has sent out the rhizoids, *w*, *w'*, *w''*. B, a flat proembryo, *p*, from the base of which a leaf-bud *k*, and rhizoids *w*, *w'*, have proceeded. The base of the proembryo often puts out a number of new flat proembryos before it proceeds to form a leaf-bud. $\times 100$. (After Sachs.)

branches of the same plant (*Funaria*) or on different individuals (*Polytrichum*, *Buxbaumia*). The analogies with the position and distribution of the stamens and carpels in the flowers of Angiosperms are obvious but misleading, except on the general point of sex-distribution; since the parts compared are themselves essentially different in the two cases.

The sexual organs themselves are very uniform throughout the Bryales, both in outline and in development. In contrast to those of the Liverworts

both have localised apical segmentation. Each antheridium originates from a single cell, and it assumes a club-like shape seated on a short massive stalk, which is initiated by a transverse cleavage in the initial cell (Fig. 58, i). The distal cell then divides by successive alternating walls to form segments disposed in two rows (ii, iii). Each segment divides periclinally (iv, v); the outer part goes to form the single-layered skin, and the inner sub-divides to form many cubical spermatocytes (vi). When ripe the walls of these, becoming mucilaginous, swell and distend the outer skin, and distal rupture follows; it is located by a mucilaginous softening of a cap of cells at the tip (viii).

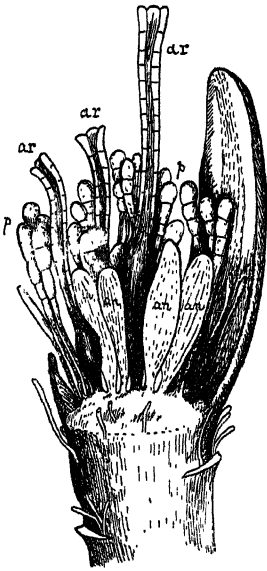


FIG. 57.

Meselia uliginosa Hedw., showing antheridia (ar) and archegonia (ar), with paraphyses (p) on the same axis. (After Hedwig, 1787.)

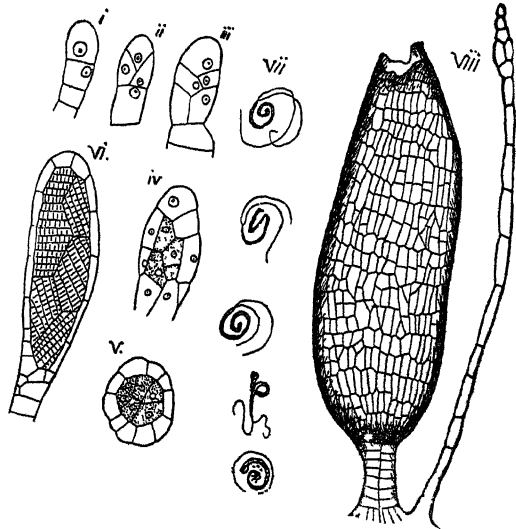


FIG. 58.

Funaria hygrometrica. Stages (i-vi) in development of the antheridium, after Campbell. $\times 400$. (vii) Spermatozooids, after Campbell and Sachs. $\times 800$. (viii) Empty antheridium of *Andropogon*, with paraphysis, after Kuhn. $\times 135$.

The pore is a small one. The contents then escape as a slow stream propelled partly by the contraction of the antheridial wall already stretched, partly by the swelling within. Finally, the bi-ciliate, spirally coiled sperms escape freely into the water which has caused the swelling (vii) (see Von Goebel, *l.c.*, p. 653.)

The archegonia of the Bryales are borne on short massive stalks; they are flask-shaped and long-necked: each of them arises from a single parent-cell. When mature the archegonium consists of a peripheral wall which is doubled in the ventral portion; but the neck consists of only a single layer built up of six rows of cells irregularly twisted; this follows naturally from the segmentation. The canal in the adult state is occupied distally by six or

more canal-cells, and below them are the ventral-canal cell and the ovum. The segmentation has been followed by various observers, but particularly in *Mnium undulatum* by Holferty (*Bot. Gaz.*, xxxvii., 1904) and by Von Goebel (*l.c.*, p. 660), from whom Fig. 59, I-IV has been taken. The development originates in a single cell, which at first undergoes alternate cleavages from a two-sided initial, forming two rows of segments, which later are bisected, giving a stalk of four rows of cells (I). This is not the archegonium

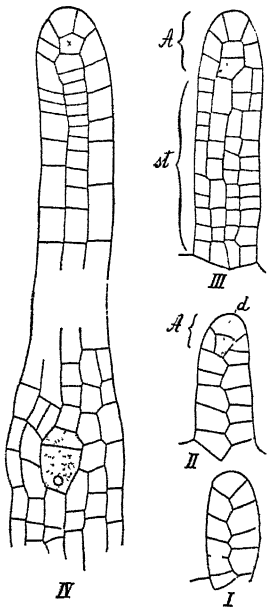


FIG. 59.

Mnium undulatum, development of the archegonium. I, primordium. II, shows the archegonium (A) initiated at its apex. III, more advanced. st, is its stalk, which is not represented in IV. (After Von Goebel.)

itself, but a sort of pseudopodium on which the archegonium is borne. Its cells retain vitality; after fertilisation they divide and form a nursing tissue at the base of the young fruit. Distally there still remains the apical cell, from which the archegonium itself arises. It assumes the form of a three-sided truncated pyramid, in which a peculiar apical growth and segmentation appears, comparable with that characteristic of the Liverworts; but differing in the fact that the cleavages are here repeated so as to give a succession of tiers of cells, instead of only one as seen in them. Segments are cut off from its three lateral faces, followed in each tier by a cell cut off from the truncate base. The neck of the archegonium is thus built up from a succession of tiers (Fig. 59, II, III). Each of these three lateral cells divides by a radial wall, giving the six rows of the neck, while the canal-cells are supplied by the cells cut off from the truncate base. The lowest of the inner series gives rise to the ventral canal-cell, and the ovum (IV).

Lastly, the cells, whether of the neck or of the central series, may undergo further intercalary growth and division, resulting in the long neck characteristic of the Bryales. This development is distinct from that in other Archegoniate Plants. It may be regarded as a further development based upon a repetition of the type of segmentation seen in the simpler archegonia of the Liverworts. It appears to hold for all Mosses with the exception of the Sphagnales.

The general facts of fertilisation need not be described here. However problematical the means of transfer of the sperms to the archegonia of land-living Bryales may appear to be, there is no doubt that it is carried out in Nature as effectively as it may be demonstrated in the laboratory, through the medium of water. But the converse question may arise in the case of Mosses

habitually submerged, such as *Cinclidotus*, *Fissidens*, or *Fontinalis*; do these normally fruit in water? They mostly live near the surface, and fruit only occasionally, but this is not due to suppression of the gametangia, for these are freely produced. It is probably due to the dispersal of the sperms by movement of the water into which they escape. Von Goebel has shown that when grown in a small volume of water in a glass *Fontinalis* fruits freely. On the other hand, the sporogonia do not open when submerged; they fall away still "cleistocarpic," but occasionally vegetative development may arise from them.¹ Such facts suggest that the aquatic Mosses do not spring directly from a submerged ancestry, but like aquatic Flowering Plants are the result of secondary adaptation to the submerged habit.

THE SPOROPHYTE OF THE BRYALES

A. The Stegocarpic Capsule

An average type of the mature sporogonium of the Bryales, as regards external form, is seen in *Catharinea* (Fig. 51); others may be larger or smaller than this, while internally they may vary in complexity. The plan of its construction is always radial, though the diameter habitually varies so as to distinguish the swelling capsule and apophysis from the thinner stalk, or seta, upon the end of which it is borne upwards. The sporogonium is inserted at its base upon the tissues of the leafy plant. The position is usually distal on a relative main axis, as in *Catharinea*; but frequently it appears to be lateral, being then borne actually on the end of a short side-branch. The capsule is covered at first by a hood or cap, the calyptra, derived from the archegonial wall, within which it is nursed. This falls off at maturity, laying bare the apex of the capsule. In *Catharinea*, as in most of the Bryales, a lid or operculum is separated at ripeness by a transverse split, and falls away: this is the essential feature of the Stegocarpic type. Thus the inner cavity of the capsule is laid open, and the numerous spores liberated: they are distributed through the agency of the peristome, which forms a fringe of teeth or bristles round the orifice. The underlying scheme of construction of the sporogonium of the Bryales, though variable within limits, conforms to a plan which is the same for them all. Variants will be illustrated later by certain selected examples: meanwhile a general type of its structure will be described, with which those variants may be compared.

The internal structure of an average sporogonium of one of the Bryales, as seen in an immature state in median section, is illustrated for *Funaria* in Fig. 60. To the left, part of the seta is seen, which widens out into the swollen base of the capsule, called the *apophysis*. This is continuous with the fertile region, the whole being of a full green colour while young, owing to the presence of photosynthetic tissue. It is bounded by a well-developed

¹ Von Goebel, *Organographie*, p. 968.

epidermis, bearing numerous stomata, especially on the surface of the apophysis. Centrally the *columella* is suspended by parenchymatous threads

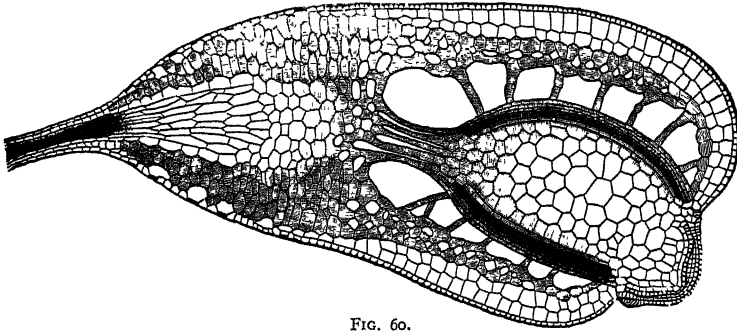


FIG. 60.

Funaria hygrometrica: longitudinal section through an unripe sporogonium. (After Haberlandt.)

within an air-space, which is nothing more than a highly distended cavity in the spongy parenchyma. The narrow seta is traversed by a rudimentary conducting strand, which widens out as it enters the swollen base of the capsule into a parenchymatous core, and this merges again into a mass of spongy parenchyma which is connected by threads of cells with the base of the columella. Thus a channel of conduction is provided leading up to the centre of spore-production. The columella appears as a solid mass of thin-walled cells, surrounded by the barrel-shaped *spore-sac*; this consists while young of a single layer of cells of the *archesporium*, enclosed within and without by smaller-celled nutritive layers. Such is the state shown in Fig. 60. But as development proceeds the cells of the archesporial layer undergo repeated divisions, and the resulting cells separate, rounding off as spore-mother-cells; finally they undergo tetrad-division. As the spores mature

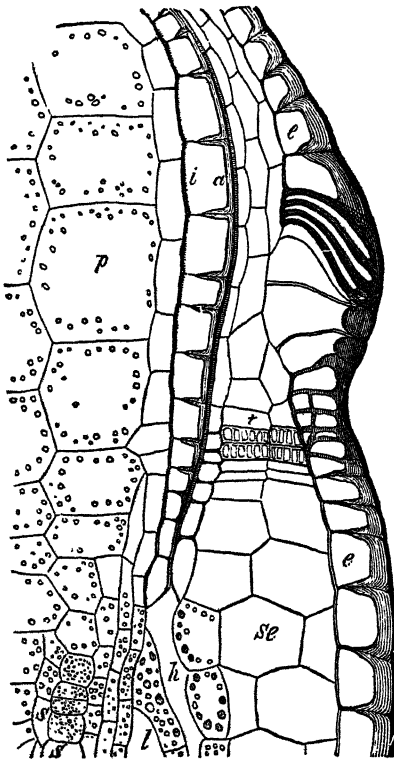


FIG. 61.

Funaria hygrometrica: portion of a longitudinal section of an immature capsule. *s* = archesporium. Highly magnified. (After Sachs.)

within an air-space, which is nothing more than a highly distended cavity in the spongy parenchyma. The narrow seta is traversed by a rudimentary conducting strand, which widens out as it enters the swollen base of the capsule into a parenchymatous core, and this merges again into a mass of spongy parenchyma which is connected by threads of cells with the base of the columella. Thus a channel of conduction is provided leading up to the centre of spore-production. The columella appears as a solid mass of thin-walled cells, surrounded by the barrel-shaped *spore-sac*; this consists while young of a single layer of cells of the *archesporium*, enclosed within and without by smaller-celled nutritive layers. Such is the state shown in Fig. 60. But as development proceeds the cells of the archesporial layer undergo repeated divisions, and the resulting cells separate, rounding off as spore-mother-cells; finally they undergo tetrad-division. As the spores mature

the remaining cells of the spore-sac and of the columella dry up, and the ripe capsule is filled with a vast number of dry and dusty spores.

Meanwhile changes appear in the apical region which are closely related to spore-dispersal (Figs. 61, 62). In the first place, a transverse ring of cells is formed, which delimits the lid or operculum from the rest of the capsule. These cells are characterised by their distended form, and in most Bryales by their mucilaginous contents. The mucilage swells with access of water and does not shrink on drying as much as the adjoining tissues. This causes strains which lead to the rupture of the capsular wall, and the whole distal cap, or operculum, breaks away, exposing the tissues within. Changes of induration have meanwhile appeared in a deeper seated layer of cells: a strip of the outer wall (α) and another of the inner wall (i) of each cell thickens, while the rest of each wall remains thin. The relation of these becomes clear by comparison of the transverse and longitudinal sections (Figs. 61, 62). Further, a ring of cells (α'), connecting these indurated strips basally with the hardened epidermis, completes a rigid system based on the outer wall of the capsule; though internal in origin this system is exposed when the operculum that covers it breaks away. Since all

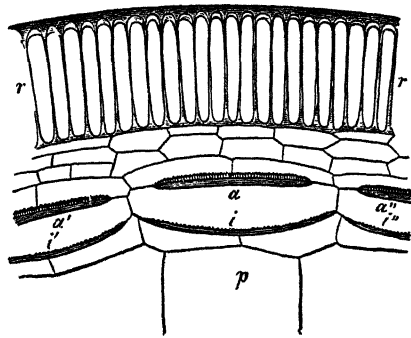


FIG. 62.

Funaria hygrometrica: portion of a transverse section through the lid. α =teeth of peristome; i =cilia. Highly magnified. (After Sachs.)

the thin-walled cells shrivel on ripening, and their weaker parts rupture, the isolated strips of indurated wall will remain as a double fringe of appendages, numbering sixteen in each series. The outer are recognised as the *teeth* of the *peristome*, the inner as the *cilia*. They show hygroscopic movements: these are normally smooth and gradual, but the strips often give irregular jerks, owing to the rough edge of one filament catching that of another till it is suddenly released. Such movements are effective in the dispersal of the spores. Such is the structure of the peristome as seen in *Funaria*. (Compare Fig. 67.)

For purposes of comparison a knowledge of the development of this complex sporogonium is desirable, as seen in any average member of the Bryales. It originates from the fertilised zygote. The first cleavage after fertilisation is by a basal wall in a plane transverse to the axis of the archegonium. This separates an epibasal from a hypobasal hemisphere, and the polarity is defined as *exoscopic*, the apex being directed towards the archegonial neck. This first cleavage is succeeded by oblique segmentations in the epibasal half, which alternate so as to define a two-sided initial with two rows of

segments (Fig. 63, A, B). The apical growth is not long continued, and gives place later to intercalary activity. The hypobasal half of the embryo

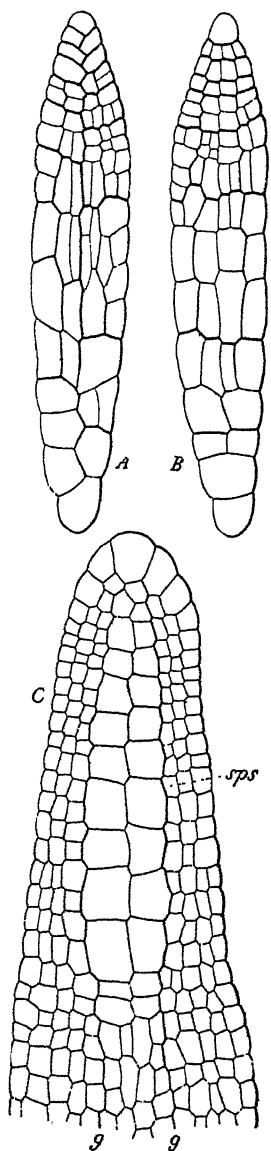


FIG. 63.

Ceratodon purpureus. A, B, young embryo seen from points of view at right angles to one another. C, an older embryo; g, g, outer limit of endothecium; sps, outer spore-sac. (After Kienitz-Gerloff.)

undergoes less regular cleavages, giving rise to the base of insertion of the seta on the parent plant. The segments of the epibasal region sub-divide with great regularity in such a way as to give rise to a relatively constant and definite result. A central tract of tissue, the *endothecium*, is formed, consisting of four rows of cells, two of which appear in each longitudinal section (Fig. 63, B, C); but all four appear in the transverse section, as seen in Fig. 47, F, G, H; they form in fact a central column of four rows, which is surrounded at first by a single layer of cells of the *amphithecium* (Fig. 47, G). In both regions further cell-division takes place, leading to the adult state: nevertheless, the limit between them remains clearly defined until the specific development of the tissues appears. The endothecium thus readily distinguished in the upper region is less clearly defined in the lower epibasal segments, which will constitute the seta; but upwards it extends throughout the part that will form the capsule, even to its apex. (Fig. 63, C). Thus the definition of the endothecium and amphithecium is not merely a local development in the part that will be ultimately fertile: it extends both upwards and downwards, beyond the limits of the fertile zone. This is fully demonstrated for *Funaria* by Campbell's drawings (*Mosses and Ferns*, Figs. 106-110): it is also shown clearly in the small Cleistocarpic Moss, *Phascum* (Fig. 64). After further segmentation of the cells forming this central column of the endothecium, it is from its outermost layer that the *archesporium* arises. A continuous and well-defined series of cells so located assume dense contents, and after further sub-division, and finally the tetrad-division, they form the spores. The developmental details thus described give a definite picture of the archesporium as a barrel-shaped

tract of fertile cells, open at both ends. Such facts offer a basis for comparison with other Bryophytes.

From a physiological point of view it is important to realise the part which the sporogonium of *Funaria* actually takes in self-nourishment. The water supply with solutes is led by the conducting tract of the seta into the apophysis, and through the columella to the spore-sac. The apophysis is ventilated by numerous stomata, and provided with a considerable bulk of photosynthetic parenchyma; this tissue is

extended, with larger air-spaces which finally merge upwards into one continuous cavity; but the surface of the spore-sac is related to it throughout by the suspending filaments (Fig. 60). Experimental proof of its success in nutrition is adduced by Haberlandt, from cultures of unripe capsules of *Funaria* isolated from the parent plant, and grown in inorganic nutrient solutions. In one case the result was that in three weeks the dry weight of the young sporogonia had increased 150 per cent., and they had matured a normal crop of spores (*Phys. Anat.*, p. 299). Thus the capsule may under special conditions be independent of the shoot,

so far as the supply of plastic material is concerned. Nevertheless, the initial supply up to a late stage is from the gametophyte that bears it.

The distribution of the photosynthetic tissue, and of the stomata so intimately related to it, is various in the several types of the Mosses. In such as may be held to be relatively primitive the stomata are numerous and generally distributed; for instance, in *Sphagnum* over 200 may be present, scattered very uniformly over the surface of a single spherical capsule.¹ This diffuse distribution is found also in some of the Bryales, but in by far the majority of these more specialised Mosses the stomata are found chiefly on the lower part of the capsule, or exclusively upon the apophysis itself; as, for

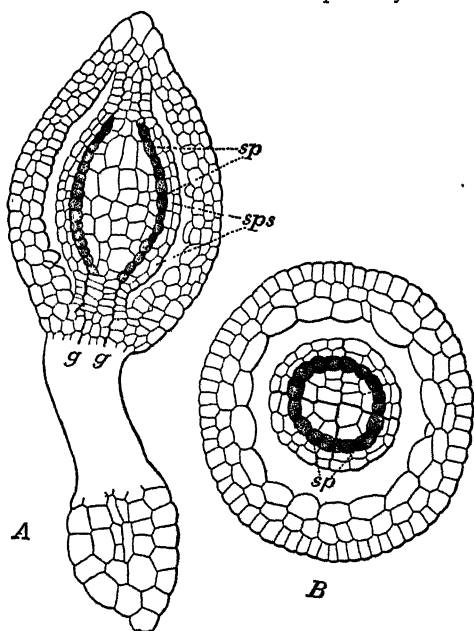


FIG. 64.

Phascum cuspidatum Schreb. Schut. A, longitudinal section through a sporogonium after formation of the air-space; *sp*, archesporium; *sps*, spore-sac; *g, g*, limits between amphithecium and endothecium. B, transverse section of the same. (After Kienitz-Gerloff.)

¹ It will be remembered that the stomata of *Sphagnum* are non-functional, having no pore. They are quoted here as showing a general distribution over the surface of the capsule. The distribution is also general in *Anthoceros*.

instance, in *Funaria* (Fig. 60). Here again the number may be about 200. But the number of stomata on a single sporogonium is usually much smaller than this, particularly where the size is minute. In the small capsule of *Nanomitrium* there are none. The size, however, is no criterion in this: *Atrichum* has no stomata on its relatively large sporogonium, and this is so also in many other genera where the fruit is of a fair average size: such as *Andreaea*, *Cinclidotus*, *Fontinalis* and *Leucobryum*. The absence of stomata,

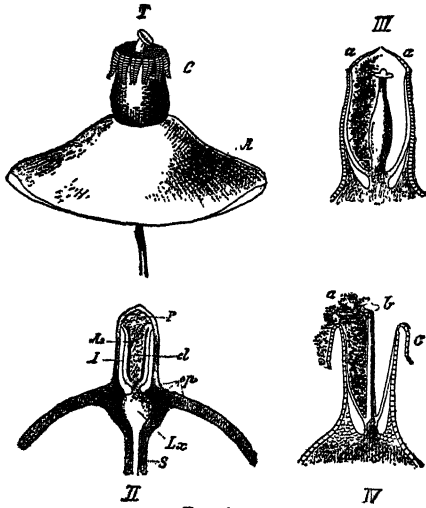


FIG. 65.

Splachnum luteum. I, capsule open. A, apophysis. II, unopened capsule in longitudinal section; s, seta; Lx, leptoxylem; sp, stomata on apophysis; cl, columella; p, peristome; As, archesporium; I, intercellular space. III and IV are diagrams to illustrate the opening of the capsule. (From Von Goebel, after Hedwig, Vaizey, and Bryhn.)

thus seen even in Mosses with relatively large capsules, may be related to the fact that imperfect stomata are common. The two guard-cells arise normally from a mother-cell by fission, and a splitting of the division-wall forms the pore. The commonest imperfection is that the pore is absent, as it is in *Sphagnum*: or the wall of partition may be partially absorbed, as in *Polytrichum juniperinum*. Many capsules show clear traces of such imperfections, which are linked with a general reduction of their photosynthetic system.

There is a marked tendency in many Mosses towards a dissociation of the photosynthetic and the fertile regions, notwithstanding that these often remain in some degree geographically related. The apophysis itself owes its origin to this, as is seen in *Funaria*, where the mass of chlorophyll-parenchyma and the stomata occupy a region distinctly below the spore-sac (Fig. 60). But the climax of this dissociation is reached in the Splachnaceae, where the apophysis is often larger than the capsule itself. In *Splachnum luteum* it appears as a wide frill-like expanse, which shows a structure not unlike that of a leaf-blade, with well marked and cuticularised epidermis covering a spongy mesophyll. But the stomata are here restricted to a limited zone of the upper epidermis, where they are grouped closely round the insertion of the capsule (Fig. 65).¹ In all

¹ It has been suggested that the office of the enlarged apophysis of *Splachnum luteum* is not primarily nutrition, and it has been pointed out that many of its stomata are defective (Von Wettstein, *Oesterr. Bot. Zeitschr.*, Bd. 50, p. 651). It may well be that by its yellow colour and even by its odour the apophysis may prove effective in spore-distribution by attracting dung-flies. But still the fact remains that the structure is that of a photosynthetic organ (see Vaizey, *Ann. of Bot.*, vol. v., 1890, p. 1). Moreover, defective stomata are often present on sporogonia to which no such attractive features are ascribed (see Von Goebel, *l.c.*, p. 1029).

such cases the nutritive region is based upon the amphithecium : the endothecium—which is often expanded for water-storage—may take a minor part ; but its most distinctive function is to give rise to spores, and in the Bryales this last duty is restricted to it.

The stomata of Mosses are of a relatively simple type. They resemble those of certain Dicotyledons in preserving a constant width, and, as Haberlandt notes, there is no hinge-mechanism. Consequently the total length and breadth of the stoma remain constant during physiological action. Notwithstanding these rudimentary features they are efficient in control, by changes in the width of the individual guard-cells according to turgor. As this increases, the outline of each cell in section tends to become circular, and the surface bounding the pore straightens and is withdrawn; as the turgor relaxes that surface resumes its strong curvature and closes the pore (Fig. 66).

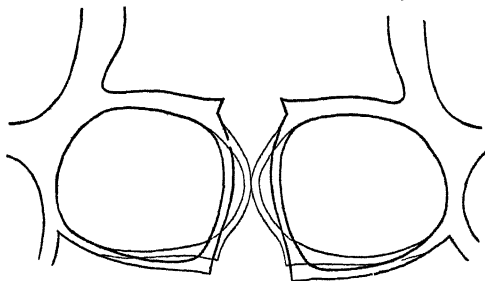


FIG. 66.

Diagram showing a stoma of *Mnium cuspidatum* in the open (heavy lines) and in the closed (faint lines) condition, as seen in transverse section. (After Haberlandt.)

The description here given has been mainly based upon an average type of the Bryales, viz., *Funaria*. It may be amplified by a brief description of certain other examples, chosen so as to illustrate the sort of variants of form and structure which Mosses show, and particularly of the mechanical arrangements for spore-distribution. As a first example *Georgia* (Ehrh., 1780) may be taken : this genus is better known as *Tetraphis* (Hedw., 1782). Our common British species, *T. pellucida*, is a small Moss, growing in dense tufts an inch or less

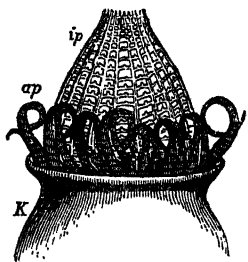


FIG. 67.

Apex of capsule (*h*) of *Fontinalis*, after shedding the operculum. *ap*, outer peristome ; *ip*, inner peristome. (After Schimper.) $\times 50$.

in height, on turfy banks or in woods, and particularly on rotten tree-stumps. It shows in its protonema as well as in the structure of its capsule features which are held as pointing to a relatively primitive position. The germinal tube is filamentous, but its lateral branches widen habitually into a flattened, often spatulate form, as the so-called "protonemal leaves"; the leafy plant springs from the base of one of these (Fig. 56, II, B). Other developments may take the form of those "protonema-bäumchen"

which originate from irregular branching of a highly segmented but ill-defined axis. The special interest of these unusual developments lies in their comparison with similar growths of the protonema in other Mosses also believed to

be relatively primitive, such as *Sphagnum* and *Andreaea* (Figs. 40, 44). The value of this comparison is enhanced by the fact that other genera more or less nearly allied to *Tetraphis* show similar flattened protonemal expanses: for instance, *Oedipodium*, and *Diphyscium*. The infrequency of such thalloid

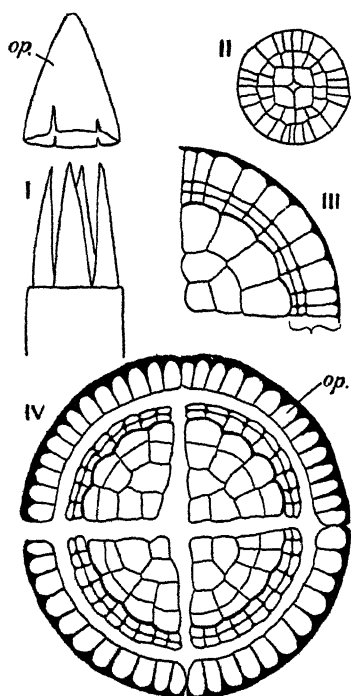


FIG. 68.

Tetraphis pellucida. I, upper portion of a ripe capsule, with four peristome teeth; above is the detached operculum, *op*. II, Transverse section of young capsule, taken above the annulus; the four central cells (columella-portion of the operculum) have already split apart. III, Transverse section of upper portion of nearly ripe capsule: the outermost layer of cells forms the operculum. IV, Transverse section of operculum and peristome of ripe capsule, in which the operculum (*op*) has become loosened, and the four teeth have split apart. (II and III from Von Goebel, after Cavers)

expansions of the protonema among other Bryales adds weight to these comparisons, and still more the fact that the genera named bear other signs of a primitive state.

The peristome of *Funaria* has been seen to consist of a double row of bristles, sixteen in each row, originating from a definite layer of cells with specially indurated inner and outer walls; these separate as pairs of strips that show individual hygroscopic movements. Modifications of this are not infrequent in the Bryales: an example is seen in *Fontinalis*, where the inner row forms a connected lattice-work (Fig. 67). On the other hand *Tetraphis* (with some other relatively primitive Bryales) is exceptional in that the peristome consists of only four, relatively massive, teeth, ranged in a single series: they are exposed when the operculum breaks away (Fig. 68, I). The operculum here consists of a single layer of indurated cells (IV. *op*). The whole mass of tissue enclosed by it divides into quadrants, forming four solid masses; the planes of their fission correspond with marginal splits seen in the lid. When moistened these

teeth close together, but when dry slits open between them through which the spores escape. Such a peristome differs widely from the mere strips of indurated wall, as seen in most of the Bryales. But illuminating comparisons may be made with the Splachneae. Here, in *Splachnum* itself, the single peristome of sixteen teeth arises from three layers of cells; the teeth themselves are more or less united at the base, often in pairs, and are very hygroscopic (Fig. 65, I). In *Tetraplodon*, as in *Tetraphis*, the teeth of the peristome appear to be four, but they are actually ranged in four double pairs. The imperfect segregation of the teeth in such

cases points in the direction of the smaller number. On the other hand the allied genera *Oedipodium* and *Schistostega* are gymnostomous, having no peristome at all. Clearly the characters of the peristome in the Bryales are variable, and their details do not strictly follow those upon which the systematic grouping is based ; but they do point to a basal number of four. In this connection Von Goebel cites as an analogy the Liverwort *Cyathodium*, in which a small operculum is detached, while the indurated wall below separates into eight teeth which are hygroscopic (*l.c.*, p. 672, Fig. 653).

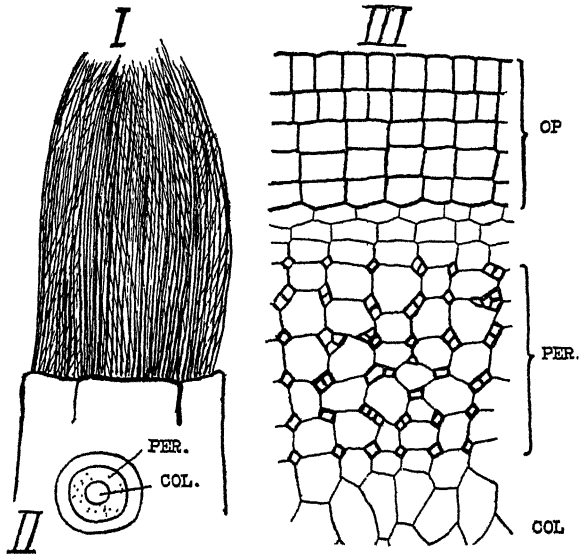


FIG. 69.

Dawsonia. I, Upper portion of capsule, with peristome of numerous bristle-like processes II, Transverse section of upper portion of young capsule, showing the relatively broad peristome-forming zone. III, a portion of II, magnified to show the narrow thick-walled cells, and the wide thin-walled cells of the peristome-zone. The former produce the peristome-teeth, the latter break down. Outside the peristome-zone is a layer of thin-walled tissue, which breaks down when the operculum becomes detached. (After Cavers; II and III are from Von Goebel.)

Further comparisons may be made with the Jungermanniales, where the capsule splits habitually into four valves. The number of teeth of the peristome, or of cleavages of the capsules, is in all these instances some power of two : such numbers as 4, 8, 16, 32 and 64 are known. As to origin, they may probably be related to the primary segmentation which underlies the structure of all of these sporogonia. It seems to be immaterial whether the primary cleavages in the embryo be transverse, as in Liverworts and in *Sphagnum*, or by alternate segments from a distal two-sided wedge, as in the Bryales ; provided the further cleavages be such as to give in transverse section a rectangular division into quarters. It is this radial structure that lies at the back of all these developments, including also the four longitudinal slits of dehiscence in *Andreaea* (Fig. 46). In no large group of Land Plants

is the adult structure so definitely related to embryonic cleavages as in the Bryophyta, and particularly in their sporogonia.

A further variant is seen in the complicated structure of the large capsule of *Dawsonia*. The peristome is here represented by a "pencil" of bristles, which arise from a broad zone of tissue composed of rows of narrow thick-walled, and of wide thin-walled, cells. As the tissues dry up the former separate as individual teeth (Fig. 69). They are hygroscopic, and approach one another when moist, like the bristles of a wet brush; but they separate

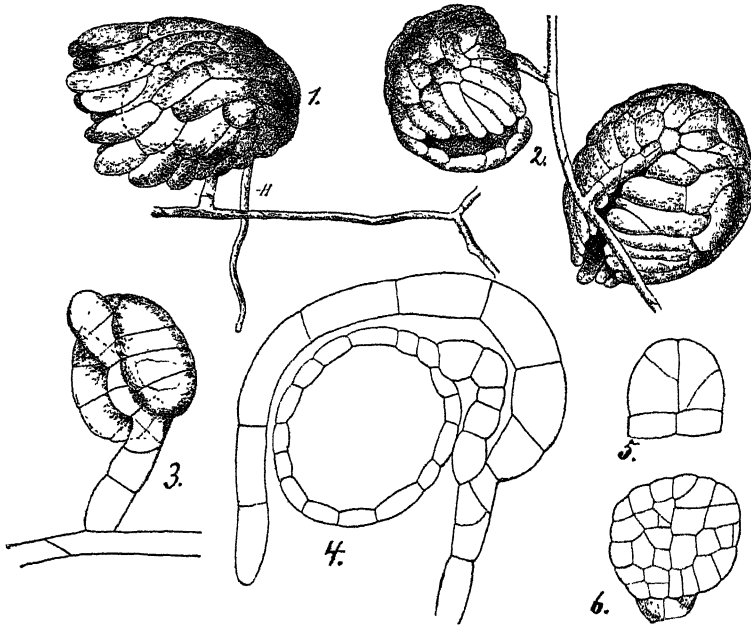


FIG. 70.

Buxbaumia indusiata. 1, Protonemal filaments bearing a male plant. H, a rhizoid. $\times 220$. 2, The same with two male plants, one in anterior, the other in posterior view. 3, a young male plant more highly magnified. 4, semi-diagrammatic longitudinal section of a male plant. 5 and 6, cell-nets of young leaves. There is no two-sided apical cell, such as is present in other Mosses. (After Von Goebel.)

on drying. This state appears to be structurally related in origin to the well-known drum-head mechanism of the capsule of *Polytrichum*, in which, when its operculum falls away, a membranous epiphragm is exposed, attached by numerous claw-like peristome-teeth, 16 to 64 in number. As in *Dawsonia*, these are not merely strips of membrane, but they consist of curved bundles of thickened fibrous cells. There are open pores between them, like the perforations of a pepper-pot, and the spores are slowly dusted out by shaking in the wind. This biological end is secured in the Bryales through the very varied development of the inner tissues above the spore-sac; these follow lines of specialisation which are all based upon a plan that is uniformly radial. In this plan the Liverworts and the Mosses are essentially alike, but the

actual dispersal is aided by parts which are quite distinct in the two Classes. In the Liverworts elaters are usually the active agents : in the Mosses no elaters exist. Their place is taken mechanically by parts derived from the capsular wall, and particularly by the peristome, of which a few examples have been described above.

The opportunity for its action is given by the separation of the operculum in the Stegocarpic Bryales. A comparative study of their spore-distribution has been made by Von Goebel (*l.c.*, pp. 1025-1034) ; the problem is solved in very various ways by them : moreover these may be different within a single family. But they all coincide in securing that the numerous small spores shall be only gradually set free. The methods show some degree of analogy

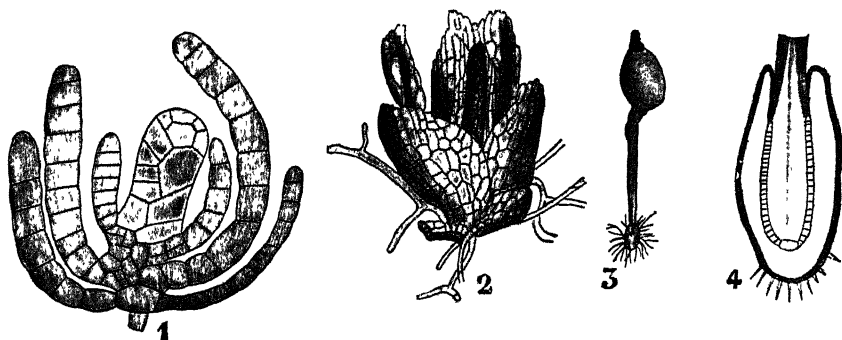


FIG. 71.

1, 2, *Buxbaumia indusiata*. 1, young female plant, with a few leaves, and one terminal archegonium, in longitudinal section. 2, female plant which is arrested in consequence of absence of fertilisation. (After Von Goebel.)

3 and 4, *Buxbaumia aphylla*, after Haberlandt. 3, strong plant with dorsiventral capsule : the stem bears colourless leaves and rhizoids, and appears as a sheath enveloping the sporogonial foot. 4, longitudinal section through the tuberosus stem (freed from the mat of leaves), with the sporogonial foot. (From Von Goebel.)

with the methods of pollination or of seed distribution in Flowering Plants, in that use is made of the ordinary forces of Nature, though these are aided by special mechanical devices. But only one example of the use of animal agency is known among Mosses : viz., in the Splachnaceae. Here the enlarged apophysis is not only brightly coloured, red or yellow, but it also emits odour attractive to dung-flies, and these in visiting the moss-grown faeces of deer and other rodents convey the sticky spores thence to new soil suitable for the development of these curiously specialised Mosses.

THE BUXBAUMIACEÆ

Variations in the balance of the leafy plant and of the protonema have already been mentioned (p. 75). An extreme example which raises interesting questions of nutrition is seen in *Buxbaumia*. The British species, *B. aphylla*, is gregarious, growing on humus-soil, in woods or on hillsides. The annual plants spring from an extensive protonema that is green where exposed to the light, but it extends rhizoid-like far into the soil. Such filaments resemble fungal

hyphae, and like them the branches anastomose freely together while, as in other Mosses, they are closely related to the organic debris which they permeate. The leafy plants borne upon them are dioecious. The male plants are very minute and simple, and have few rhizoids, or none: each consists of a single distal, long-stalked antheridium, ensheathed by a single colourless leaf; there is actually no stem (Fig. 70). The female plants are more highly

organised, as naturally accords with their maternal function. Each consists of a minute stem bearing a distal archegonium, or sometimes two; several colourless leaves form a covering for the archegonium and the young embryo: from their fimbriated margins green protonemal filaments may be formed (Fig. 71). The sporogonium is as large as that of *Polytrichum*; its oblique capsule is borne up on a seta half an inch or more in length, the base of which is enveloped in the stem, now enlarged as a tuber (Fig. 71, 4). Structurally this tuber consists of a corky external coat that covers a storage tissue rich in protein and oil-drops. Thus supplied with nourishment in its younger stages from below the capsule itself is developed later as an efficient photosynthetic organ. Its fundamental structure is according to the type usual for the Bryales; but as it matures the capsule borne upon the erect seta takes an oblique position, while the photosynthetic tissue is strongly developed on its upward side. This gives a very characteristic lop-sided appearance to the

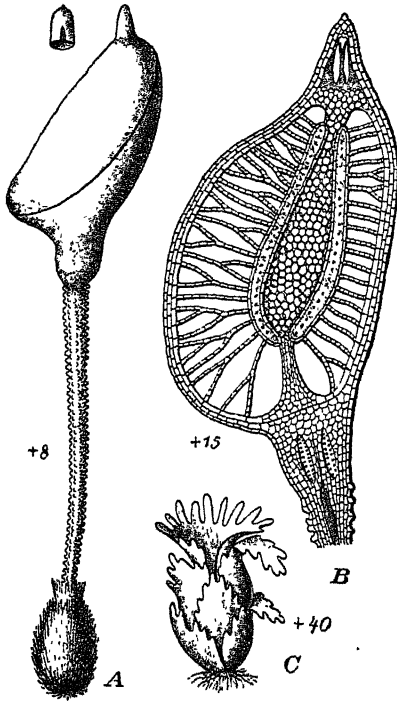


FIG. 72.

Buxbaumia aphylla L. A, Fruiting plant, $\times 8$. B, longitudinal section through the capsule, $\times 15$. C, sterile plant, $\times 40$. (After Limpricht, from E. and P., *Nat. Pflanzenfam.*, Bd. II., 1925.)

slightly flattened head (Fig. 72). The related genus *Diphyscium* shares the main characters of *Buxbaumia*; but the leafy plant is more fully developed, the female having relatively large green leaves, which do not bear that marginal protonema so often present on those of *Buxbaumia*. Both genera possess a relatively extensive rhizoid-system, extending into fine hypha-like branchings, and forming those complicated anastomoses already noted. In addition to these peculiarities the exposed protonema of *Diphyscium* bears peculiar discoid and stalked assimilating organs; but they do not appear to give rise to leafy plants, as in *Tetraphis*: these spring from ordinary protonemal filaments. The sporogonium of *Diphyscium* is again large, and the capsule oblique, but it is almost sessile. Its insertion on the gametophyte calls for remark, for the base of the short seta bears haustorial rhizoids, a feature

shared by some few other Bryales (Fig. 73). This is, however, a marked feature in the Anthocerotales, and as will be seen later it is characteristic also of the embryo of *Tmesipteris* (see p. 138). The method of dispersal of the spores in *Diphyscium*, which it shares with *Buxbaumia*, is also noteworthy. The dehiscence is by a small operculum, which as it falls away lays open a narrow channel of exit for the spores. The pore is further guarded by a pleated and funnel-shaped curtain, having a still narrower opening; it arises from the innermost layer of the amphithecium, and is peculiar for these genera. In *Buxbaumia* there are also found vestiges of a functionless outer peristome. The capsule on ripening presents a large area of thin membranous wall, which originally covered the bulky photosynthetic tissue now dried up. The result is that, yielding to the slightest wind-pressure, the whole mechanism acts as a bellows, the stream of air pressed out through the narrow nozzle carrying the minute spores with it. Again a gradual and intermittent dissemination is the result, though the mechanism is different from all others.

These characters of the Buxbaumiaceae are thus in many ways exceptional. They raise among other questions that of their nutrition, and in particular that of the relative parts taken by photosynthetic self-nutrition, and by saprophytic supply, with the possibility of a reflex effect in reduction of size or structure as a consequence of the latter. The close application of the rhizoids of the Bryales to the organic constituents of the soil is itself suggestive, though no complete proof of their solvent action upon organic debris has yet been given. But it is a well-known fact that certain Mosses thrive better, and some of them live exclusively, on certain organic soils; for instance, *Tetraphis* prefers rotten wood, while *Splachnum* and *Tetradontium* are found on the faeces of rodents, *Tetraplodon* on the faeces of carnivores, and *Buxbaumia* on humus, particularly in woods. Such facts are suggestive, though not conclusive, of some degree of saprophytic nutrition. But though

indirect nutrition may exist, it is habitually supplemented in the Mosses by direct photosynthesis. *Buxbaumia* is, above all others, a case in point. Both its male and female plants are photosynthetically negligible, though they may owe something to a green protonema, and yet the one produces an antheridium, while the other affords sufficient nourishment, through the tuberous sheath that enfolds the base of the seta, for the supply of a rela-

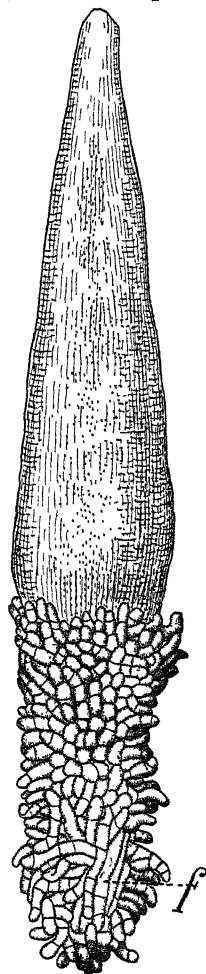


FIG. 73.

Diphyscium foliosum. An embryo dissected out, with its haustorial rhizoids; at *f* is a damaged spot. (After Von Goebel.)

tively large capsule until the latter has carried its own photosynthetic system to functional maturity. Such facts, taken together with the fungoid fusions of the finer rhizoids, afford a basis for the probability of some degree of saprophytic nutrition. It remains for the question to be tested by pure cultures, suitably controlled. Till such tests have been made it would be premature to draw definite conclusions as to morphological reduction, such as habitually follows on indirect nutrition. In any case, however, we do see in the male plant of *Buxbaumia* the simplest known form of Moss Plant, and that among the Mosses the Buxbaumiaceae present the strongest available evidence in favour of some degree of saprophytic nutrition. On the other hand Dr. Rayner (*Mycorrhiza*, chap. ix., p. 173) remarks that : " In general it may be concluded that there is practically no evidence at present for the existence of anything in the nature of a mutualistic relation with fungus mycelium in Mosses as a whole, while the claim for its existence in certain specialised genera, e.g., *Buxbaumia* and *Tetraplodon*, lacks experimental confirmation."

B. The Cleistocarpic Capsule

Certain of the Bryales in which the sporogonium is small, and its structure relatively simple, raise questions of reduction in the diploid phase. Such Mosses in which the spore-output is often greatly restricted have been distinguished as *Cleistocarpic*, because they do not open by an operculum as is the case with those having larger capsules, which have been styled *Stegocarpic*. The simpler structure follows usually on a small size of the leafy plant. The first impulse would naturally be to regard their simplicity as an indication of a primitive state : this view has been widely held, and has been expanded by comparative argument based upon much detailed observation. But in such matters an alternative view is always possible, viz., that the simplicity is consequent on reduction. Any conclusion as to these alternatives must be based on a careful balance of the available facts.

The Cleistocarpic Mosses cannot properly be regarded as a coherent group : they have in fact been distributed by good authorities among various families of Stegocarpic character, on the ground of general comparison apart from this special feature. Consequently they can only be compared loosely one with another, as isolated examples of the structure which they show, each type contributing its own evidence to a general conclusion. A few examples treated from this point of view will therefore suffice. Among the Pottiaceae, which are tufted Mosses of various size but mostly small, the genera *Acaulon* and *Phascum* are minute, and are characterised by the absence of any operculum. *Phascum cuspidatum* has a stem about one line long, with crowded erect leaves in which the minute capsule is immersed, bearing a conical calyptra. It is a plant of variable size, common on clay banks and fallow fields. The detailed development of its sporogonium has been followed by Kienitz Gerloff (*Bot. Zeit.*, 1878, p. 36). The first cleavages are after the type usual for the Bryales, and they lead to the distinction of an

amphithecium and an endothecium. The former provides the capsular wall and the outer-sac, the latter gives rise to the columella surrounded by the archesporium, which as usual is derived from the outermost layer, and is of barrel-shape (Fig. 64, p. 87). The seta is short, and stomata may be present, but there is no indication of an operculum, or of a peristome. In the allied genus *Pottia*, however, both are usually developed though variable, moreover the annulus in *Pottia* is sometimes ruptured, sometimes persistent; the peristome is often absent, or rudimentary (Engler u. Prantl, *Natürl. Pflanzenfam.*, Bd. 10, 1924, p. 289). Such signs of variability in an allied

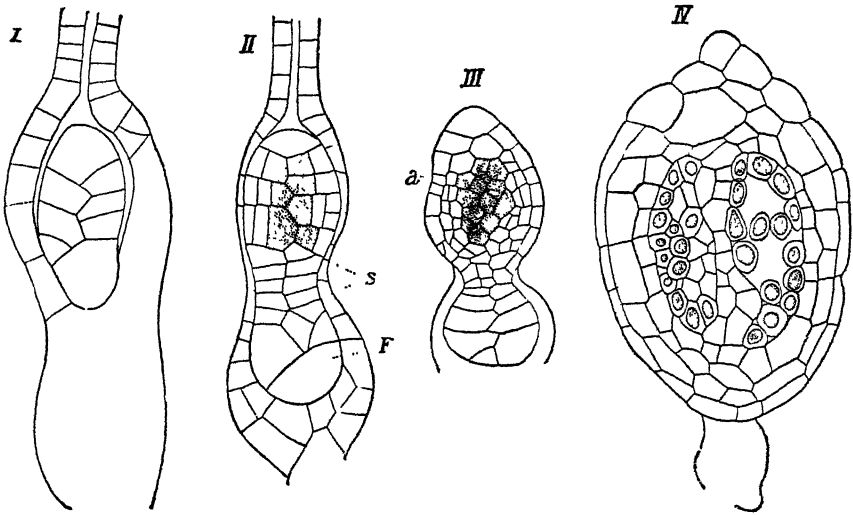


FIG. 74.

Nanomitrium tenerum. Archegonium after fertilisation, and young sporogonia at different stages of development, in longitudinal section. In II, the endothecium is shaded. F, foot; s, stalk. IV, sporogonium showing the sporocytes for the most part separate round the columella. All magnified, I the most highly. (After Von Goebel.)

genus are of interest for comparison with *Phascum*: they suggest that those parts are absent in the latter genus through a progressive reduction already indicated in *Pottia*. The spores are set free by rotting or by rupture of the wall. The structural analogies which exist between the sporogonium of *Phascum* and that of *Andreaea* hold notwithstanding the difference in dehiscence. The most interesting is in respect of the archesporium, which is a complete dome in *Andreaea*; but in *Phascum* the continuity is broken at the apex. Moreover, the definite column of the endothecium is continued beyond the limits of the fertile zone. (Compare Figs. 45 and 64.)

Another simple cleistocarpic type is seen in *Nanomitrium* which, together with the related genus *Ephemerum*, is placed systematically in the Ephemeraceae in close relation to the Funariaceae. They are small soil-growing Mosses with persistent protonema and a very short stem bearing few leaves, and they are usually dioecious. The seta is short and the capsule ovoid, with or without

stomata. The columella usually disappears at ripeness, and there is no peristome. There is in *Nanomitrium* a rudimentary annulus, but not in *Ephemerum*. The development of the capsule has been worked out for *Nanomitrium* by Von Goebel (Fig. 74). The segmentation of the embryo begins on the plan usual for the Bryales (I), and the differentiation of the endothecium and amphithectium follows; below is a narrow seta and enlarged foot (II., III.). The endothecium after further division of its cells differentiates

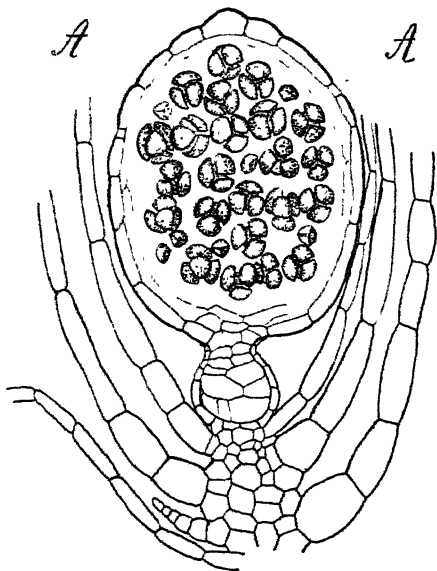


FIG. 75.

Nanomitrium tenerum. Longitudinal section through an almost ripe sporogonium. A, annulus. The spores are still associated in tetrads; the cells of the amphithectium are, with the exception of the wall-layer, almost all dissolved; the columella has disappeared entirely. $\times 120$. (After Von Goebel.)

into an exiguous central columella, surrounded by relatively numerous and somewhat irregularly arranged spore-mother-cells (IV.). As maturity approaches the columella disappears, its materials having served to nourish the relatively large spores which fill the cavity. At ripeness the appearance is as in Fig. 75. Here in section the annulus may be recognised in the small cells of the single-layered wall that are marked (A). It is also readily visible externally, and in *N. synoicum* those cells appear to define a line of cleavage of an operculum. The genus *Ephemerum* differs from *Nanomitrium* in the absence of any definite operculum; the condition of the columella is the same, but while it disappears at maturity in some species (*E. papillosum*), in others it may still be seen in the mature capsule (*E. crassinervium*). The fact that stomata occur on the capsular wall, though when ripe this is only a single layer in thickness, has its bearing on the

question whether or not these simple Mosses are primitive or reduced; favouring the latter view.

Another cleistocarpic type of doubtful affinity is seen in the genus *Archidium*. Here the capsule of the Bryales is seen in its simplest state. The genus consists of small Mosses which perennate by means of a buried protonema and stolon-like branches. The leaves are awl-shaped and numerous but the perichaetial leaves are broader. The capsule, which is inserted by a peg-like foot, has neither stomata nor columella; the spores are very large, and are set free by irregular rupture, or by rotting of the wall. Though the primary segmentation in *Archidium* is as in the Bryales the development shows that in transverse section the endothecium is represented on a reduced scale, by only two cells in place of the normal four. Moreover, there is no clear distinction between columella and archesporium. But all the endothecial cells are not fertile; some 2 to 7 become spore-mother-cells, and the spore-output

is accordingly only 8 to 28 (Fig. 76). These are, however, of unusually large size, while the remainder of the cells of the endothecium are obliterated in the course of their development. Thus the condition seen in *Archidium* may be compared with that already described for the Liverwort *Notothylas* (p. 16). Without suggesting even remote relationship between plants so diverse in general features, both of these show how individual cells produced from the endothecium may be either sterile or fertile.

Another peculiarity of *Archidium* is that the air-space which intervenes in other Bryales between the spore-sac and the sporogonial wall is continued as a complete dome over the apex of the columella, while there is no initiation of an operculum; nor is there any seta, but only a peg-like haustorium at the base. As Von Goebel remarks (*l.c.*, p. 1018), all these characters point towards a far-reaching reduction, and there is no indication of primitive characters in *Archidium*.

Two alternative views may be considered as to the evolutionary position of these Cleistocarpic Bryales. Either they may be held to be relatively primitive as compared with the great mass of kindred types, or they may be regarded as reduced forms. The balance of evidence appears to be in favour of the latter interpretation, and the chief reasons for this conclusion are as follows. First, all of these Cleistocarpic Mosses are small, some of them are

very minute indeed. Their spore-output is relatively low, while the spores themselves are in extreme cases unusually large; this is especially so in *Archidium* (Fig. 76); but it is in marked contrast to those in most Mosses, where the spores are minute, and scattered to the wind by elaborate mechanical devices. These large spores are not suitable for such distribution; atrophy of the mechanism might then be anticipated. The small size of these Mosses affects both the gametophyte and the sporophyte; the size of the capsule being fairly balanced to that of the leafy plant. This points towards a generally depauperate condition rather than to a primitive state of the capsule itself.

Secondly, there is in none of the cleistocarpic Mosses any specialised mechanism that is effective in spore-distribution, such as is characteristic of other Bryales. But there are in varying degree vestigial signs, such as an annulus indicated only by a line of smaller cells (*Nanomitrium synoicum*), though even this appears to be absent in other species of the genus, as it is also in the allied genus *Ephemerum*. Further, in the Pottiaceae, while in *Phascum cuspidatum* there is no indication of either operculum or peristome, both of these are usually present in the allied genus *Pottia*; though here

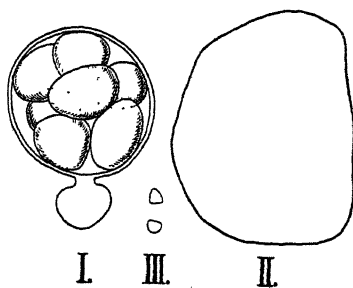


FIG. 76.

I, Sporogonium of *Archidium phascoides* with the spores outlined. II, one spore of *Archidium* more strongly magnified. III, two spores of *Dawsonia superba* drawn to the same scale as II. (After Von Goebel.)

there are already signs of variability and inefficiency in both. These vestigial indications point collectively towards reduction rather than to a primitive state. A like conclusion follows from comparison in respect of the stomata ; these may even be present on a sporogonial wall which when ripe consists of only a single layer of cells (*Ephemerum*). On the other hand the relations of the fertile cells to the columella in *Nanomitrium*, and its final obliteration in *Archidium*, are also more readily intelligible as phenomena of reduction than as indicating an ascending sequence of elaboration.

The most cogent evidence, however, lies in the fact that the Cleistocarpic Bryales do not form a natural group. Their affinities are rather widely spread. This fact is readily intelligible if their simplicity of sporogonial structure be held as resulting from a depauperate existence, such as their small size itself suggests. Thus the conclusion may be reached that the evidence favours a theory of reduction for them all.

Though the Bryales include a vast number of genera and species their general facies is remarkably uniform, however great may be their variety of minor detail. Particularly is this so for the sporophyte, which constantly retains its fundamentally radial construction. The Bryales are in fact a very natural assemblage of organisms. That conclusion follows from any general survey, notwithstanding that the preceding descriptions have for the most part dealt specially with outstanding and divergent types, rather than with those which make up the staple of the Moss-Population.¹

The near relation of the Bryales as a whole to the Sphagnales and Andreaeales cannot reasonably be held in doubt. Together with them they constitute the natural Class of the Musci. But just as the Sphagnales and Andreaeales present features which justify their separation from the Bryales, and indicate for them an intermediate position between the Liverworts and other Mosses, so in a less marked degree certain of the Bryales may again be segregated from the rest on the ground of features that compare specially with the Orders just named. These may be held as relatively primitive, and as occupying a middle place by comparison on the one hand with *Sphagnum* and *Andreaea*, and on the other with the main mass of the Bryales. Three Sub-Orders stand thus apart from the rest, which may be styled the Eu-Bryales. They are the Tetraphidales, the Buxbaumiales, and the Polytichales. The features upon which this segregation is primarily based are : (i) the mode of development of the protonema, in particular whether or not flattened expansions are present ; and (ii) the presence and nature, or the absence of a peristome. If, for instance, the protonema is liable to be widened into flat expansions, and in the same plant the peristome be of a

¹ For further details regarding these reference must be made to standard systematic works, such as the *Natürliche Pflanzenfamilien* of Engler and Prantl, vols. x., xi., 1924-5 ; or, for British Mosses, the *Student's Handbook* by Dickson and Jameson ; or to Verdoon's *Manual of Bryology*, 1932.

relatively massive type, these two quite distinct features, either of which is held to mark a primitive organisation, would mutually support the conclusion that the Moss which shows them is itself relatively primitive. If only one of these features be present its comparative value will be less, though still not negligible. Probably the types of Bryales which show them represent each a separate line retaining primitive features, though all are based upon a uniform life-cycle and plan of construction. Putting these exceptional types aside, with a general sense that they are relatively primitive, there remains the vast mass of the more uniform genera and species. But this is not the place to enter on any detailed discussion of their inter-relationships, for which reference should be made to systematic works.

CHAPTER VI

COMPARATIVE SUMMARY FOR THE BRYOPHYTA

CERTAIN leading types of the Bryophyta have been discussed in the preceding Chapters. The descriptions have not related specially to one or the other of the alternating phases of the life-history, but to both : for the whole life-cycle should be brought into the field of comparison, as a basis for general organographic conclusions. In the period immediately following the publication of the *Origin of Species* it was customary to assume that relatively simple types were primitive until the contrary should have been proved. For instance, the Leptosporangiate Ferns, and particularly the Hymenophyllaceae, were assumed to be the most primitive of their Class. But more exact comparison and a better knowledge of the related fossils has shown that assumption to be untenable. A similar preconception has dominated the evolutionary outlook of many botanists upon the Bryophyta. Collectively they certainly are the simplest of the Archegoniatae, and it has been assumed that among the very simplest of the living Bryophyta the key should be found to the evolution of the first Land Plants. It is only in recent years that this assumption has been called in question. Before a decision can be reached they must be examined more critically than hitherto. We may ask whether or not the simple state which so many of them present may not have followed as a result of retrogressive biological change. Professor Von Goebel has provided in his elaborate studies of the Bryophyta not only a wide area of material facts, but also a running commentary of criticism that greatly aids other morphologists in coming to a decision. His own opinion is stated thus : " Provisionally the view that we have before us in the Bryophyta a group which cannot be linked with others, either upwards or downwards, seems best to accord with our present knowledge. Further, it is a group in which numerous reductions, in the historical sense, have taken place" (*Organographie*, iii. Aufl., Teil ii., pp. 643 and 1038). These reductions have been tabulated by him under twenty-four heads, and they relate to all the main divisions or orders of the Class (*l.c.*, p. 1035) ; moreover, they affect both the haploid and the diploid phases. Together they convey a pervading sense of progressive reduction as a recurrent feature of the Class. The descriptions given in the preceding Chapters, which have been largely based upon the work of Professor Von Goebel himself, provide salient instances. The question will

then present itself as to the probable balance between initial elaboration and subsequent simplification.

Fundamental for any such discussion must necessarily be some clear understanding of the interdependence of nutrition and propagation. The propagative processes demand a supply of material for their normal course ; that supply in green plants will be by photosynthesis, which either precedes or runs concurrently with propagation in any completed life-cycle. The two functions are not necessarily separate in time or in space : in forms that are relatively primitive they are usually concurrent. This is seen in the simpler Algae, or in the *Selago*-type of the Lycopods. It is in a more advanced state that they are liable to be separated. Progressive segregation of this nature has ultimately led to such a state as is seen in the Higher Flowering Plants. In the comparative study of the Bryophytes a like question of segregation will have to be considered, whether in respect of the haploid or of the diploid phase, or of both. Those types, or their parts, in which the two functions coincide, may be held as relatively primitive ; those in which they are partially or even completely separate would rank as relatively advanced. On the other hand, the possibility is always to be reckoned with in any specific case that, by a throwback, an earlier but disused function may be resumed, and their dissociation blurred.

Applying such views to the Bryophyta, one Order of the Liverworts stands out distinctly from all the rest as imperfectly segregated according to function, viz., the Anthocerotales. Neither in the haploid nor in the diploid phases of these plants is there any sharply localised distinction between the regions that are photosynthetic and those that are propagative. In all other Bryophytes the segregation of the nutritive and propagative functions is more or less marked. In particular, the sporogonium in the remaining Liverworts is habitually colourless, and specialised as a spore-bearing and distributing body ; and photosynthesis is carried out only by the gametophyte. On the other hand, in the Mosses, while the Moss-plant is habitually photosynthetic, that function is in most of them carried out also by the sporogonium ; but only in a minor degree. At first the individual Moss-sporogonium is certainly not photosynthetic ; the foot and seta are already advanced in development before the nutritive tissues localised in the apophysis or in the capsule itself become functional. The capsule is at first delayed in its development, and it is only when it is passing on to spore-formation that self-nutrition in relation to it becomes active. Occasionally at this late stage the apophysis and even the capsule itself are specially developed for the purpose, as in *Splachnum* *Diphyscium*, and *Buxbaumia* ; and there is reason to believe that in them this region may account for a considerable proportion of the organic material used in the later stages of spore-production. But such developments are probably of late and specialised origin, in fact, of the nature of a " throw-back." In their young sporogonia the functional segregation of the Mosses

is of the same order as that of the Marchantiales and Jungermanniales, in which photosynthesis is absent altogether from the sporogonium (Chapters II, III).

The segregation of photosynthetic and propagative regions in the gametophyte, whether of Mosses or of Liverworts, is less decisive. It attains its most marked development in such Mosses as *Mnium* or *Polytrichum*, and in the Marchantiales among the Liverworts. The whole range of such facts gives interesting parallels with familiar features in Vascular Plants, though with details essentially different. The same principle of progressive segregation underlies them all, whether Vascular Plants or Bryophytes.

One of the consequences of progressive segregation, acting on a generalised structure such as a primitive Bryophyte sporogonium, would probably be imperfect development on the one hand of the propagative, and on the other of the photosynthetic system. Evidence of this would appear most clearly about the limits of the differentiated zones. Such anticipations account in the Bryophyta for facts which would otherwise be difficult of interpretation. The clearest indications of reduction of the photosynthetic system appear in the frequent existence of *imperfect and non-functional stomata*. Instances have been quoted in Chapters I, IV, and V. These stomata, with their various degrees of imperfection, occupy the same position as effective stomata in related forms. Such facts are best explained as evidence of some previous state where ventilation had existed, and a final result would be total absence of stomata, which is a common state in Mosses. Support of this view is found in the similarity in the steps of elimination in families so remote as the Anthocerotales and Bryales. On this point the conclusion of Von Goebel runs thus: "There is no doubt that many Moss-capsules show clear traces of a reduction of the photosynthetic system, and of the stomata closely related to it—all this indicates that Moss-sporogonia originally possessed a structure similar to that of *Anthoceros*" (*Organographie*, p. 1025; also Figs. 926 and 1099-1101).

Turning now to the Bryophyte archesporium, similar questions arise on comparing the limits of this propagative tract as they are defined by the initial segmentation, with the actual realisation in the development of spore-mother-cells and spores. The result of such comparison is that frequent signs are found of *progressive sterilisation of tissues*: that is, the diversion of cells or cell-masses of the fertile tract in the course of their maturation to other uses than direct propagation. The whole argument is based here upon the early definition of the archesporium, which in all Bryophytes appears as one continuous tract of tissue. Where the sporogonium is oval or approximately cylindrical, and of limited size, this tract occupies a central position within the protective wall, and this was probably the original state for them all. Early segmentation habitually defines an inner endothecium from an outer amphithecium (Figs. 39, 63, 64). As a rule the former, in whole or in

part, becomes the archesporium ; the latter forms the protective wall. It is from the former that the spores originate in all of the Liverworts excepting the Anthocerotales, and in all of the Mosses excepting the Sphagnales. There are no Classes of Plants in which the changes following on sterilisation present such interesting material for comparison as do the Liverworts and Mosses. This is a natural consequence of the monangial state of the individual sporophyte, and of the necessity for highly specialised use of so limited a scheme. The evolutionary problem before the Bryophytes has been to exploit, without branching and in a single season, the simple fertile cyst, distal in position, and with a solid core: the end has been to secure a large output of spores adequately nourished, and to distribute them in the most advantageous way. But the Classes of the Liverworts and Mosses differ in their method of meeting this demand for distribution of the spores ; the Liverworts have elaters while the Mosses have none. Accordingly, while the archesporium of the Mosses presents a coherent tract of cells all devoted to spore-production, that of the Liverworts is relatively diffuse, owing to the association in various ways of sterile cells that form elaters with the spore-mother-cells. The two types will be best considered separately, and then compared.

In the Marchantiales and Jungermanniales the whole of the endothecium may be fertile, excepting those widely diffused cells which form elaters, or elaterophores. Originally all alike, the cells that form elaters are early distinguishable by their elongated form from the spore-mother-cells (Figs. 20, 21). In the Marchantiales the elaters are usually diffuse and unattached ; but in the Jungermanniales they are disposed with some degree of regularity, and are often attached to the wall of the capsule : thus they are mechanically effective in the scattering of the spores when the capsule bursts, and its valves are everted. In large capsules a further step is sometimes seen in the massing of sterile cells to form a solid elaterophore, attached either at the distal end of the capsular cavity (*Aneura*), or at the basal end (*Pellia*) (Fig. 38). A study of the development indicates that the elaterophore results from a progressive sterilisation of archesporial cells (Fig. 39). A comparison of this with the sterile columella of *Anthoceros* or of the Mosses seems to lie near to hand ; but it cannot be closely drawn, and in none of the Jungermanniales does a complete columella exist, traversing the capsule from apex to base.

In most of the Anthocerotales the continuous sterile columella terminates in a rounded dome, while the archesporium completely overarches its tip and ensheaths it. The endothecium is here wholly used up in forming the columella. The archesporium is derived from the innermost layer of amphithecial cells ; it yields as in other Liverworts not only spore-mother-cells but also elaters of relatively simple structure. Both columella and archesporium may be extended indefinitely below by the activity of a basal

intercalary zone (Fig. 7). If the larger genera of the Anthocerotales alone existed it might be difficult to bring this structure into relation to that of other Liverworts. But in the relatively small sporogonium of *Notothylas* there may be no columella, or various degrees of an imperfect state may appear (Fig. 9). The development of *Notothylas* shows that an endothecium is formed as usual by the initial segmentation, but that any cell of it may develop as a spore-mother-cell. This makes it appear probable that originally the whole endothecium was sporogenous in the Anthocerotales, as it probably was in all other Liverworts; but that in the larger representatives fertile cells were wholly replaced by sterile cells, while the office of spore-production was transferred to a more superficial position, viz., to the innermost layer of the amphithecium. We thus see that the primary segmentation does not lay down an immutable barrier between sterile and fertile development. A tissue that is as a rule fertile may in special cases be in part or in whole sterile, while the office of spore-production may be assumed by a tissue that is as a rule sterile. The result of comparison in the Liverworts is thus to show a certain latitude in the balance and position of sterile and fertile tissue, with a marked tendency at times towards sterilisation at the centre, so as to form a columella. But this was never completely carried out so as to become a general feature in them, as it is in the Mosses.

In the vast majority of the Mosses the archesporium has the form of a barrel open at both ends. It consists of a coherent simple layer of cells which after subdivision are all fertile. It is embedded in specialised tissues serving purposes ancillary to spore-production. The distended central columella, which is here a continuous column, appears chiefly as a water-reservoir. The external tissues are protective and in varying degree photosynthetic, especially in the basal region of the capsule, or below it, where it is expanded as the apophysis. The distal region above the limit of fertility is specialised in relation to spore-distribution, as the operculum and peristome. The capsule is thus a more highly elaborated structure than in the Marchantiales and Jungermanniales.

The primary segmentation, with continued apical growth in the more elaborate types, results in an inner column of the endothecium covered by the many-layered amphithecium (Figs. 63, 64). With remarkable constancy it is from the outermost layer of the former that the archesporium arises. But the fertility of its cells is limited above and below, though the definite archesporial layer of cells may be traced as extending beyond those limits in both directions (Fig. 77). On the other hand, the irregularity of the inner limit where the archesporium adjoins the columella, as compared with its outer limit, confirms in certain cases their common origin from the endotheciums (Fig. 45). Such developmental facts suggest that the barrel-shaped fertile tract is a residuum left after curtailment by sterilisation.

Originally there probably was a solid fertile endothecium with a domed

apex, which was surrounded by a sterile protective wall. That it was so may be held as a reasonable working hypothesis. The original sporogonium was probably of a simple spindle-like form, as it is still seen to be in all young sporogonia (Fig. 63). Internally the distinction of endothecium and amphithecium may be traced downwards from the distal region that will form the capsule into that which will form the seta. The first external change is the enlargement of a zone below the capsule, forming the apophysis, which at this stage may be greater in diameter than the capsule itself (Fig. 77, A). In typical Bryales the archesporium is from the first a single layer of cells surrounding the sterile columella. It is suggested that the originally solid fertile tract has been decentralised, so as to form the sterile columella, leaving only the outermost layer fertile. Some degree of probability for this is yielded by the fact that occasionally cells of the columella have been seen to be fertile in *Barbula* and *Bryum*, while the same has been noted in injured sporogonia of *Funaria*: it is even suggested that this state may be experimentally produced (Von Goebel, *l.c.*, p. 1019). On the other hand, various degrees of fertility of the columella exist in the Cleistocarpic Bryales, and these have been brought into comparison as evidence of its originally sporogenous character. The biological importance of the columella as a reservoir of water and soluble substances is a sufficient justification for its presence normally as a sterile tract.

The barrel-shaped archesporium fades off at the base, losing its sporogenous character. This suggests that its cells have been sterilised in relation to the enlargement of the photosynthetic apophysis, and that this has defined a lower limit of fertility (Fig. 77, c). The argument for sterilisation at the apex of the domed archesporium is, however, stronger. There is reason to believe that the distal dome was complete in the progenitors of the Bryales. This is actually seen in *Andreaea*, a relatively primitive type of Moss in which the dehiscence is by longitudinal slits, not by an operculum, and it is significant that it has no peristome (Fig. 46). There is also a complete dome in *Sphagnum*; here again, though an operculum is formed, there is no peristome, and the spores are ejected by one sudden explosion. The nearer the

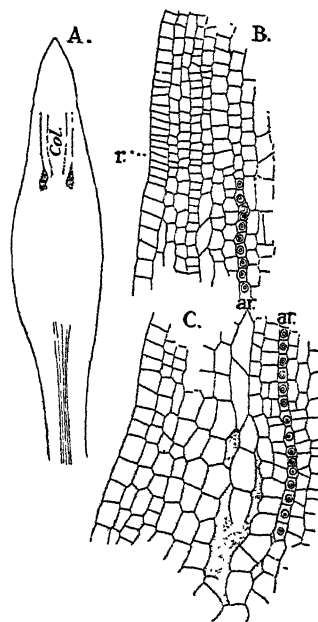


FIG. 77.

Funaria hygrometrica. A, longitudinal section of a sporogonium showing the first differentiation of its parts, $\times 48$. B, the upper part of the same, $\times 300$. r, marks the limits of theca and operculum. C, basal part of capsule of the same, $\times 300$. ar, archesporium; col, columella. (After Campbell.)

spores lie to the opening the more effectively will they be scattered ; in this the occasional persistence of the complete dome may find its justification (Fig. 43). But in the normal Bryales it is incomplete (Figs. 60, 61). This goes along with the presence of an operculum and of a peristome. The fertile archesporium stops short immediately below the base of the peristome and annulus. It may well be that the development of the one is complementary to the other, and that the expenditure of material upon annulus and peristome may have been causally related to the arrest of fertility in the distal region of the domed archesporium. Biologically the spore-sac thus truncated suffices for all needs, while the accessory tissues add to its mechanical efficiency.

The distributing mechanisms in the Bryales, in relation to which this sacrifice of the distal fertility appears to have been made, are far the most elaborate seen in the Bryophyta. They secure an ample spread of the spore-output over time and space. In both of these respects the Bryophyte type is otherwise inherently deficient: for the sporogonia are sedentary, of low stature, and with the exception of the Anthocerotales, the maturing of the spores in each capsule is simultaneous. But if, retaining their vitality, the spores are shed in successive showers, not all at once, the chances of successful germination will be greatly enhanced ; while the variable strength and direction of the wind that conveys them, when shed at successive intervals of time, will increase their spread. Thus the distal arrest of the domed archesporium, and its substitution by a distributing mechanism, may be held as remunerative. And so we may contemplate as probable, both morphologically and biologically, the curtailment of the archesporium as seen in the most advanced Mosses.

At the best, however, the Bryophyte type is fore-doomed to small dimensions. It is true that the gametophytes of some of them are the most elaborate that exist among land-plants ; but even these do not bear the elements of further advance beyond what is actually seen in the largest of them. The leafy plant of *Dawsonia* may, in fact, be held as the climax of its effective realisation. On the other hand, the simple sporogonium is the correlative of the branched vascular sporophyte. We may ask what are the reasons for this difference. The Bryophyte sporogonium has certain obvious disabilities, which may account for its remaining relatively small. The chief of these are, its continued physiological dependence on the gametophyte, with self-nutrition at best feeble and for the most part of late occurrence in the individual. Further, the absence in the Liverworts of localised apical growth, and its early arrest in the Mosses ; also the absence of lateral appendages, and of branching except as a rare abnormality. Another disability consists in the integral continuity of the archesporium, while the spore-sac itself is non-septate. A simultaneous spore-development follows naturally in all except the Anthocerotales. The effect of each of these disabilities is serious

enough, but their collective effect suffices to account for the failure of the individual sporogonium to progress beyond a limited size. What is lacking is the combination of certain factors of advance to a common end. With apical growth regular branching should be associated; with photosynthetic activity a direct supply of salts from the soil; with a high spore-output a plurality of independently ripening spore-sacs, thus securing a spread of the physiological drain over a long period. Any or all of such combinations would have led to a greater efficiency.

A combination of some importance, which has succeeded in plants of higher organisation though the Bryophytes have failed to take full advantage of it either in gametophyte or in sporophyte, is that between elaboration of external form and internal ventilation. It has been seen in Chapters II and III how the presentation-surfaces of the photosynthetic thallus of the Marchantiales tends to be upheld by its chambered structure, while in the Jungermanniales the same end is secured by the foliar habit: that the two series had diverged in structure, holding firmly either to the one or to the other, but that neither had combined the two methods. In the evolution of the Mosses the same problem of maintenance of proportion of surface to bulk will have presented itself, particularly in the larger types. In the gametophyte it is met in the first instance by the leafy habit, but in the leaves of some of the largest of them the difficulty has been still further eased by upgrowths from the surface. These certainly increase the proportion of surface exposure, though they may bring other advantages as well. Nevertheless, the result even in the Polytrichaceae falls far behind that of the ventilated leaves of Vascular Plants. On the other hand, the sporophyte of Mosses commonly possesses stomata, and ventilated photosynthetic tissues; but being without branching or appendages it cannot make full use of that structure, except by variants on the prevailing cylindrical form, such as the expanded apophysis. We thus see that neither phase of the life-cycle in the Bryophytes has secured full photosynthetic efficiency, by combining elaboration of external form with ventilation of photosynthetic tracts. Their stunted habit is itself a witness to their lack of morphological initiative in this matter.

Among the living Bryophytes it is in the Anthocerotales that the most promising signs are seen; in particular, they are endowed with intercalary growth, while *Anthoceros fusiformis* may sometimes approach physiological independence of its sporophyte. Its chief deficiencies lie in the absence of apical growth and of branching. Given these and an independent sporophyte a real future might have opened before *Anthoceros*. It is one of the mysteries that surround these strange plants that, while apical growth is present in their gametophyte it is absent from the sporophyte. Before basal intercalary growth alone no morphological future seems to be open. Thus arrested by want of co-ordination of the factors of advance the Bryophyte type seems to stand apart among land-living plants. As a Class they appear morphologically stranded and alone.

The outcome of the comparisons contained in the foregoing Chapter

will be to focus attention upon the type of the Anthocerotales as relatively primitive among the Bryophytes. The step required above all others for the advance of their sporophyte, so that it should rank with that of the simplest Vascular Plants, is the converse of encapsulation, viz., the achievement of physiological independence. Increase in size and elaboration of external form, by branching or by enation of appendages, or by both, together with the development of a specialised system for absorption and conduction, and some form of origination of numerous sporangia, might then be expected to follow as natural stages in the consolidation of that independence. It is with such rational anticipation that we may proceed to the comparative study of the Pteridophyta.

But there is one further point that emerges from the comparison of the sporogonia of Bryophytes which has its importance, whether in the general morphology of the sporophyte or in the more special comparison of the Bryophytes with the Pteridophytes. It relates to the position of the archesporium. An original type for the Bryophytes probably had a solid core of sporogenous cells. In the Pteridophytes it will be seen that the spore-production is referable in origin not to deeply seated, but ultimately to superficial cells of the plant body. Moreover, in the Bryophytes, excepting the Anthocerotales, the spores are produced simultaneously in the single capsule, whereas in Vascular Plants, excepting the simplest of them, the spore-production is successive, from many capsules produced as a rule in sequence. During the period of the physiological drain in their nutrition the central tissues cannot be dispensed with, as they so often are in the Bryophytes; they must be elaborated as channels of nutrition for the later-formed sporangia and spores. A position of the archesporium near to the surface of the more massive and differentiated body is thus essential, not only in respect of easy dispersal of the spores but also for supply of nourishment from the internal conducting tracts. Hence the broad difference between the centralised archesporium of the Bryophytes, and its superficial origin in the Pteridophytes, becomes biologically intelligible. How, and in what various ways, this superficial position may have been attained in Vascular Plants will be considered later, when the facts necessary for an opinion are before us.

CHAPTER VII

PSILOPHYTALES ¹

IN passing to the Pteridophyta, or Vascular Cryptogams, the treatment of the subject must necessarily change. The study of the Bryophyta is almost wholly based upon the observation and comparison of types now living. The reason for this is that their fossil history is very defective. Till a recent date there was no detailed knowledge of Bryophytes existent as fossils in the primary rocks ; even now the evidence of structure of those early types that are known is too scanty for detailed comparative use ; nevertheless the demonstration by Walton is sufficient to prove the existence of Carboniferous Bryophytes, both Liverworts and Mosses, and to show that the form presented by them was essentially similar to that of certain living types. This confirms us in attributing to those Classes a relatively primitive position, though their comparative treatment must needs be based upon living types. But when we turn to the Pteridophytes the study of fossils bulks very largely, and the evidence has increased rapidly in recent years both in volume and in detail. This greatly adds to the interest, and indeed to the confidence felt in comparison of the living types ; for the existence and stratigraphical sequence of fossil types yields positive data, and these are invaluable in checking comparisons of a slender or an imaginative type. Such discipline tends to consolidate opinions as to the morphological interpretation of the Pteridophytes in a way that at present cannot be applied for the Bryophytes.

The succession in which the several Classes of the vascular plants will be taken for study and comparison is necessarily arbitrary. The general view is adopted that there may have been a plurality of evolutionary lines, advancing independently from a more primitive to a more advanced state.

¹ *Selected Literature on the Psilophytales* : Dawson, *Report Geol. Survey of Canada*, 1871. *Geol. History of Plants*, New York, 1888. Halle, *Lower Devonian Plants from Rörögen*, Stockholm, 1916. Kidston and Lang, "Old Red Sandstone Plants from the Rhynie Chert," *Trans. R.S. Edin.*, 1917-1921, parts i-v. Arber, *Devonian Floras*, Cambridge, 1921. Scott, *Studies in Fossil Botany*, 3rd edn., vol. i., 1920. Kräusel and Weyland, "Beitr. z. Kenntn. d. Devonflora," *Senck. Naturforsch. Ges.*, ii., 1926 ; iii., 1929, etc. Zimmermann, "Spaltöff. d. Psilophytales," *Zeitschr. f. Botanik*, Bd. 19, 1926, p. 129. Hirmer, *Handbuch d. Paläobotanik*, München, 1927. Lang, "Early Devonian Fossils from Victoria, Australia," *Phil. Trans.*, B. Vol., 219, 1930. "Spines, etc., of *Psilophyton princeps*," *Phil. Trans.*, B. Vol., 219, 1931. "*Arthrostigma*, *Psilophyton*, etc., from Caledonian Lower Old Red Sandstone," *Trans. R.S. Edin.*, vol. lvii., part ii., No. 17, 1932.

As a general rule those regarded as more primitive will be taken earlier than those that are more advanced, but even this must not be assumed to mean more than that a concession is made to convenience, pending general comparisons at the close.

The opening years of the present century have seen a great increase in knowledge of early vascular plants. This has been mainly due to the discovery of fossil types hitherto unknown, or imperfectly suggested by insufficient material. Up to the year 1900 the best-known types of the early Devonian Flora were found to be constructed of cylindrical stalks, often bearing lateral spines. These stalks were believed to have arisen from a branched creeping base. Some of them showed crozier-like curvature while young, and they occasionally bore sporangium-like bodies. But there were no broad leaf-surfaces, and the existence of true roots was doubtful. The most distinctive type recognised was the genus *Psilophyton*, of which Dawson published a reconstruction under the name of *P. princeps*: but it has been the subject of adverse criticism. Evidence of tracheidal structure has, however, been found in the fossils upon which Dawson's reconstruction was based, and from this it was concluded that they were land-plants, and that his interpretation was substantially correct.

In 1916 the examination of fresh-water deposits of early Devonian age in Norway and Sweden by Dr. Halle yielded specimens which have added greatly to the previous knowledge, while a central tracheidal strand was found in specimens referred by him to *Psilophyton princeps*: thus the land-habit was confirmed.¹ Among other plants described by Halle the most distinctive novelty was one which he designated *Sporogonites*: it consisted of a simple stalk bearing a terminal capsule, which by its form, and from the spores which it contained, appeared to be comparable with the sporogonium of the Bryophytes; but it was suggested as a generalised type, and not referable to any recognised group of them (see Fig. 439, p. 591). These most important discoveries heralded the establishment of a new Class of the Pteridophyta, viz., the Psilophytales, by Kidston and Lang. The material which they had at their disposal permitted a very complete microscopic analysis, for the parts were little crushed or deformed, as fossils so often are. This gave the new types a special value for comparison with living plants.

In 1913 there had been found at Rhynie in Aberdeenshire certain isolated blocks of chert containing plant-remains. Their source was traced by the Scottish Geological Survey to certain beds of chert of Old Red Sandstone age. An exposed land-surface had existed there subject to inundation, but periodically covered by vegetation. By its decay beds of peat were formed, over which sand was deposited. Successive layers were thus accumulated to a depth of some eight feet. Then followed water with soluble silica, probably from some fumarole, and the peat-beds were sealed

¹Halle, *Lower Devonian Plants from Rörögen*, Stockholm, 1916.

up, the plants being preserved with great perfection ; their lower parts were often found erect as in life. From this bed of chert four distinct vascular plants have been recognised and described in detail by Kidston and Lang.¹ They are all essentially similar in type, though sufficiently different to be placed in three genera, viz., *Rhynia*, *Hornea* and *Asteroxylon*. The first two are rootless and leafless ; *Asteroxylon* is also rootless, but it bears leaves of a simple type. The plants suggest a primitive state prevalent at that period. They conform in general features to the type of *Psilophyton* as described by Dawson, and as recognised in greater detail by Halle.

The four species from the Rhynie chert are referred to the three genera above named, there being two species placed under *Rhynia*. One of these, *R. major*, is the larger, though relatively simple in form as shown by the reconstruction given by Kidston and Lang (Fig. 78). Its full height is not known. It had creeping rhizomes, cylindrical and stem-like, and dichotomously branched ; they bore rhizoids on the lower surface, and sometimes on large "bulges." From the rhizomes sprang upright cylindrical stems ranging from 5 to 6 mm. in diameter to under 1.5 mm. These also branched dichotomously, tapering slightly. Some of the smaller of them were terminated by large sporangia (12 mm. \times 4 mm.). *R. Gwynne-Vaughani* was a smaller species, probably about 26 cm. in height, with the same general habit, but with certain added features. The stems were tapered from 2 or 3 mm. diam. to about 1 mm., with sparing dichotomy. Some of the lateral branches were attached by a narrow base, and being readily detachable served probably for vegetative propagation. The distal sporangia measured about 3 mm. \times 1.0 to 1.5 mm. Most of the specimens of this species bore "hemispherical projections" having oval outline, resulting from localised protuberance of cells of the epidermis and subjacent tissue (K. and L., pt. iv., p. 832). Their morphological character is obscure.

Hornea Lignieri was essentially of similar habit, but with certain differences, and with relatively low stature as inferred from the less diameter and apparently less rigidity of the stems (Fig. 79, 3). It is represented by fragmentary remains ; but among all of these plants no single specimen hitherto obtained from Rhynie shows the general habit or height. The rhizome of *Hornea* presents tuberous lobes, from each of which an erect

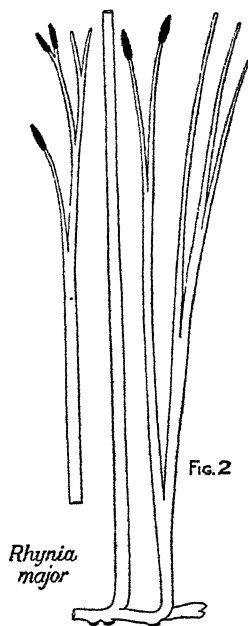


FIG. 78.
Reconstruction of *Rhynia major*,
after Kidston and Lang. Reduced.

¹ "Fossils from the Rhynie Chert, I-V," *Trans. R.S. Edin.*, 1917-1921.

stem may arise, provided with a central stele (Fig. 79 *bis*). These aerial stems bear a relation to the rhizome similar to that of the protophylls to the protocorm of *Lycopodium*, or of *Phylloglossum*, in that neither have any definite relation to a stem-apex, while each stele ends separately downwards.

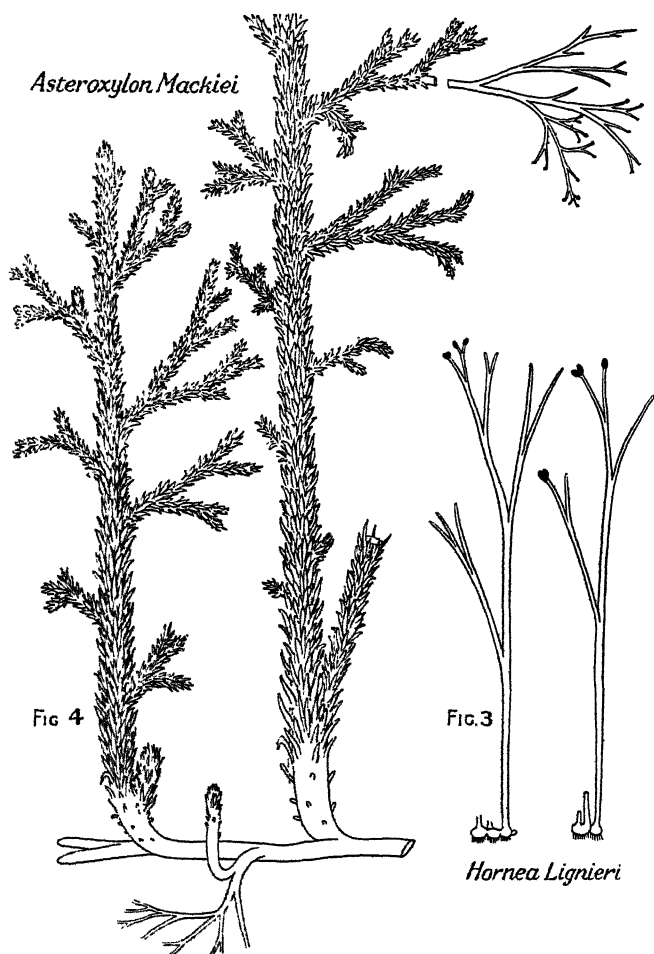


FIG. 79.

Reconstructions by Kidston and Lang of the Rhynie fossils named above. Reduced in scale.

(Compare Figs. 214, 215.) The rhizome itself is massive, and is composed of thin-walled parenchyma with intercellular spaces containing fungal hyphae. Peripherally there is a smaller-celled cortex, with an ill-defined epidermis from which numerous rhizoids spring. No vascular elements are present in the rhizome of *Hornea*, but a brown central tract of cells is associated with the base of the stele of each erect stem, which widens out into an

inverted cup-like mass of brown-walled cells. The existence of fungal hyphae in these tubers of *Hornea* appears suggestive of a mycorrhizal relation. But since certain well-preserved specimens of *Hornea* are without any trace of fungus the evidence seems more consistent with the hyphae being merely saprophytic. In *Rhynia* proof of the existence of mycorrhiza appears to be equally deficient.

The erect stems of *Hornea* dichotomised repeatedly, while some of the finer branches terminate in sporangia considerably smaller than those of *Rhynia*. The sporangia may stand singly or in pairs; they possess a central

b.t.



FIG. 79 bis.

Vertical section through the Protocorm of *Hornea Lignieri*, with rhizoids, embedded in peat. $\times 14$. (After Kidston and Lang.) The dark streaks are the brown tissue at the base of each stem. *b.t.* = termination of stele.

columella, and they may themselves be actually involved in the dichotomy of the branch-apex which has produced them. The distended and lobed rhizome, the presence of a columella within the sporangium, and the fact that the fertile region including the columella may be involved in the distal branching, are notable features. They will all take their place in the comparative discussions which arise from the proved existence of these remarkable types (Fig. 83 bis).

The fourth of the Rhynie plants is the largest, and it is of a higher order of complexity, viz., *Asteroxylon Mackiei*. The relative proportions and the connection of its parts are inferred in the reconstruction, no complete specimens having been found (Fig. 79, 4). There is a dichotomously branched leafless rhizome without absorbent hairs; its finer branchlets penetrate the fragments of plants in the peat in which it grew. There is a gradual passage upwards from the larger trunks of the rhizome to the erect stem, which becomes clothed with simple leaves. These make their appearance in the

transition region as minute scales, successively enlarging upwards. There is occasional dichotomous branching of the larger leafy shoots, but this contrasts with the predominantly lateral relation of the branches on most of the main axes. In the latter, and in the finer ramifications dichotomous branching prevails. The leaves on the main stems and branches are closely crowded, and may attain a length of 5 mm. The vegetative shoot must have had much the same appearance as that of some species of *Lycopodium*. The general habit seems to have resembled the impressions designated *Thurso-phyton Milleri*, of the Middle Old Red Sandstone¹; indeed the similarity is so great as to suggest that the two fossils may be only different conditions of preservation of one species (K. and L., iv., p. 852). The fertile region ascribed to this plant has not been found in actual connection with it, and this fact is indicated in the reconstruction (Fig. 79, 4). The sporangia were borne distally on repeatedly dichotomous, leafless branches which may be styled the *Hostimella*-twigs. The sporangia were solitary, relatively small and pear-shaped, with distal dehiscence.

The reconstruction of the Rhynie species of *Asteroxylon* by Kidston and Lang has been supported in essentials by the study of impressions on slabs from the Devonian of the Rhine valley.² Upon these Kräusel and Weyland have based a reconstruction of another species, *A. Elberfeldense*, a plant of considerably larger size (*Frontispiece*). The added features of most importance are, the circinate curvature of the distal ends of branches, and the attachment of the thin leafless "*Hostimella*" twigs to the main trunk. Though the sporangia were for the most part not found attached to them, occasional instances showed that attachment to be distal, as in the twigs ascribed to *A. Mackiei*. Thus the general features of *Asteroxylon* are now assured from two distinct sources. It will be seen later that the type of vegetation which the Rhynie plants present finds its counterpart in other archaic vascular plants of the present day.

INTERNAL STRUCTURE

Sections show the structure wonderfully preserved in the silica of Rhynie, so that the tissues can be read almost as in a section of some living plant. Fig. 80 shows an aerial stem of *Rhynia major* about 3 mm. in diameter in transverse section. Superficially lies the well-marked epidermis, with thick outer walls and cuticle. It bears stomata sparsely scattered on the aerial stem, but they are absent from the rhizome. They are not depressed below the general level. Two or three succeeding layers of clear cells form the

¹ Arber, *Devonian Floras*, Camb. Univ. Press, 1921. Fig. 10, after Nathorst. The bodies represented in his Fig. 11 as sporangia are now believed to be not of that nature.

² Kräusel and Weyland, "Beitz. z. Kenntn. d. Devonflora," *Abh. Senck. Nat. Ges.*, Frankfurt, 1926, 1929, etc.

narrow outer cortex or hypoderma, which presents no striking features, and it merges into an inner cortex composed of rounded cells with large intercellular spaces; there are indications of this tissue having been photosynthetic. The stele throughout the plant is protostelic; it is not delimited by any layer recognised as endodermis or pericycle, and is composed of a central core of tracheides surrounded by a zone of phloem. The latter contrasts with the cells of the surrounding cortex by the smaller diameter of its

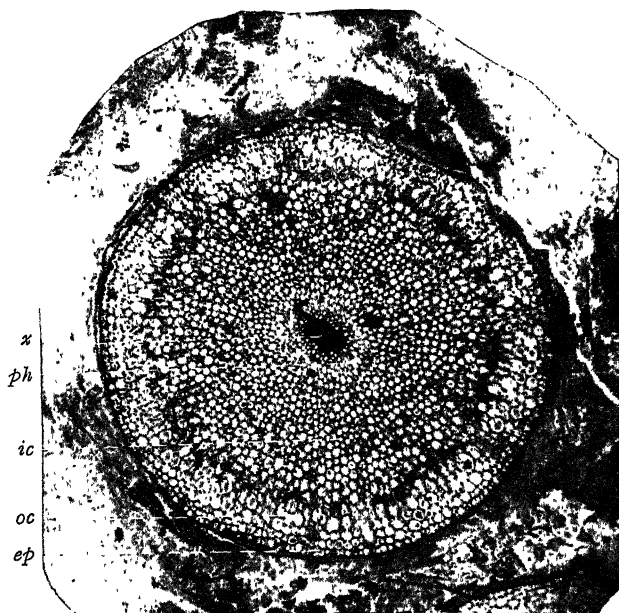


FIG. 80.

Rhynia major, aerial stem in transverse section. *x* = xylem; *ph* = phloem; *ic* = inner cortex; *oc* = outer cortex; *ep* = epidermis. $\times 14$. (From Scott's *Studies*, after Kidston and Lang.)

thin-walled elements. It consists of elongated cells with oblique ends; but sieve plates have not been found. A solid strand of xylem occupies the centre, all the tracheides composing it being alike in having broad annular thickening. Neither spiral nor scalariform marking has been seen: there is, however, a distinction in size between smaller central and larger peripheral tracheides (Fig. 432, Chap. XXVIII). This protostelic structure, though differing in minor detail, is general for *Rhynia* and *Hornea*. These plants are threaded from end to end by a vascular protostele so constructed. At a dichotomy of the stem the stele also forks; but in the adventitious lateral branches of *Rhynia Gwynne-Vaughani* there appears to have been no vascular connection with the main axis.

In the larger and more elaborate plant of *Asteroxylon*, the stems of which range from 1 cm. to 1 mm. in diameter, the vascular system is struc-

turally more advanced. As before, the main trunks of the plant, both rhizomes and aerial stems, are threaded through by the protosteles. Points of special interest lie in the details of the stele, and in its connection with the appendages; also in the superficial cortex and epidermis. The structure in the large as in the small specimens of *Asteroxylon* is primary, and was determined once for all in development. Starting from the outer surface the well-marked and cuticularised epidermis bore stomata (Fig. 81). The pores were specially large in those about the transitional region from rhizome to



FIG. 81.
Stoma of *Asteroxylon Mackiei* in surface view.
× 220. (From Scott, after Kidston and Lang.)

aerial stem. The broad cortex is differentiated in the aerial stem into a narrow outer zone of coherent cells, a middle zone which is marked by a trabecular or plate-like arrangement of the cells with wide intercellular spaces, and a coherent inner zone surrounding the stele (Fig. 82). Such differentiation is well known in stems of Lycopods, and particularly in *Lycopodium alpinum*.¹ The cortex of *Asteroxylon* is traversed by numerous leaf-traces, which may be followed upwards from the stelar region to the leaf-bases, but not into the projecting leaves. The stele itself is clearly contrasted with the cortex,

but seldom is there any indication of an endodermis. The section shown in Fig. 82 was taken just below a forking, as indicated by the paired stellate masses of xylem already separate. They are surrounded by phloem, particularly in the deep bays. Leaf-traces are given off irregularly from the arms of the stellate xylem, and are seen scattered through the cortex on their way out towards the leaf-bases which appear oval in section, without any vascular strand, and lie outside the sinuous outline of the stem. The wood consists only of tracheides, but here and there a distinction can be seen between groups of the smaller protoxylem elements immersed in the mass of larger tracheides at the ends of the xylem rays. The former pass out into the leaf-traces, which extend through the cortex to the leaf-bases, but no vascular tissue is present in the leaf itself, as Fig. 82 shows. The tracheides have a moderately thin wall with more or less regular annular thickening, the protoxylem being narrower. There is no trace of scalariform or pitted structure. The softer phloem ensheaths the xylem, and passes outwards with the leaf-trace to the base of each leaf. It thus appears that in their form and differentiation, and particularly in the stellate xylem, and in the presence of

¹ See Bower, *Ann. of Bot.*, vii., 1893, p. 329, where the subject is fully discussed.

leaf-traces, the vascular tracts of the large *Asteroxylon* are in advance of those of *Rhynia* and *Hornea*.

The microphylls of the Psilophytales have been the subject of special examination by Lang (*Phil. Trans.*, B. vol. 219, 1930, p. 133; also vol. 219, 1931, p. 421; also *Trans. R.S. Edin.*, vol. lviii, 1932, p. 491). This whole subject will be examined comparatively in Chapter XXVII; meanwhile it must suffice to state here that such microphylls as are presented by the Devonian fossils are not standardised, but show considerable variation both in

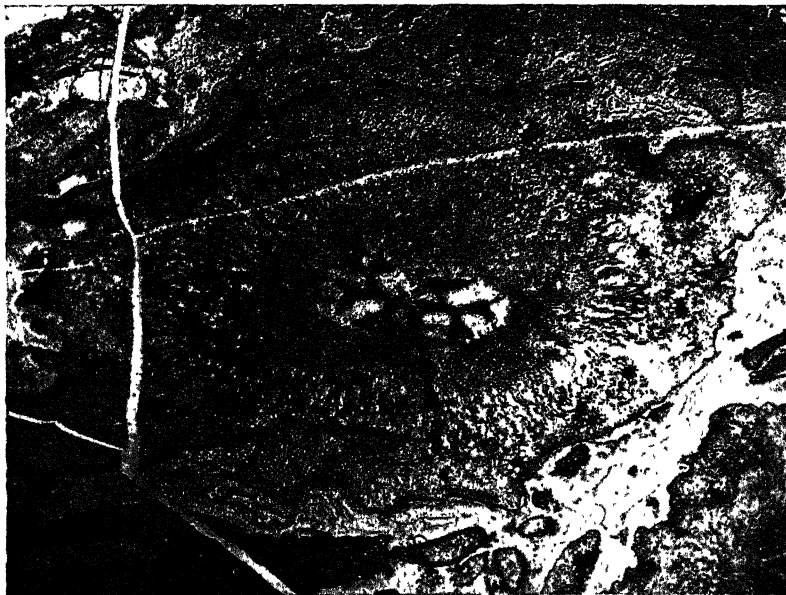


FIG. 82.

Large stem of *Asteroxylon*, cut transversely just below a dichotomy, and showing leaves attached externally. \times about 10. (From Scott, after Kidston and Lang.)

size and in complexity of structure (see Fig. 425, Chap. XXVII). The smallest microphylls of *Asteroxylon* are simply cones of parenchyma without vascular supply (K. and L., iii., Pl. iii., Fig. 23); larger examples bear stomata, while leaf-traces approach the leaf-bases but do not enter them (*l.c.*, Pl. iv., Figs. 37, 38). The microphyllous appendages of *Arthrostigma* are more spinous in character, while a strand of tracheides traverses them, surrounded by parenchyma and epidermis with stomata (Lang, *l.c.*, 1932, p. 494). On the other hand, the appendages in *Psilophyton princeps* have no vascular supply at all, though there is a vascular strand in the axis that bears them: but no leaf-traces spring from it, not even approaching their bases, as in the larger microphylls of *Asteroxylon* (Lang, *l.c.*, 1931, p. 425). Such facts may be interpreted comparatively either as evidence of reduction or of steps in an upgrade development. Considering the rudimentary character of the plants that bear them, the position which they hold on the plant-body, and the great antiquity

of the Class, the latter alternative seems the more probable interpretation. Fortunately corresponding appendages exist in the living Psilotales which will be described and compared in Chapter VIII.

The sporangia of the Psilophytales are all borne distally on certain branches of the stem, without any relation to leaves or leaf-like organs. They differ, however, both in size and in structure. The largest are those of *Rhynia major*, which may be 12 mm. in length, and 4 mm. in diameter. Each terminated a stalk similar in structure to a small stem (Figs. 78, 83). The form was cylindrical, but it tapered distally. The wall consisted of several layers of cells: an epidermis was followed by many middle layers of the wall, and there was a persistent tapetum of one or sometimes two layers;



FIG. 83.

Sporangium of *Rhynia major*, filled with spores. $\times 5\frac{1}{2}$. (From Scott, after Kidston and Lang.)

the latter invests the cavity, which contained numerous spores, frequently still grouped in tetrads, and all alike (homosporous). The epidermis was continuous over the surface with no indications of lines of dehiscence. The sporangia of *R. Gwynne-Vaughani* were much smaller. Those of *Hornea Ligneri* were also distal, as though by transformation of the end of the stem, and this impression is confirmed when, as sometimes happens, the change to sporangial structure affected a nascent dichotomy, the branching being evident in the construction of the sporangium, which then appears lobed. Each contained a central columella composed of elongated thin-walled cells, which give its tissue a fibrous appearance. It corresponds in position to the stele of the stalk; structurally it resembles the phloem of the stele with which it is continuous. It stops short of the distal end of the cavity. Where the sporangia themselves are lobed the columella is also forked; thus the sporangium as a whole shares this feature with the sterile endings of the branches (Fig. 83 *bis*). The sporangia ascribed to *Asteroxylon* appear to have been borne on slender branched leafless axes of the *Hostimella* type. They were about 1 mm. in length, pear-shaped, and with definite dehiscence at the wider free end.

All the plants described appear to have been homosporous : no stages of germination of the spores have been seen, nor has the gametophyte as yet been found belonging to any one of them.

The Psilophytales are now by far the best known of the early Devonian fossils, and they therefore take the foremost place for comparison of primitive forms with plants still living. New discoveries are, however, following in quick succession, but they are chiefly represented only as impressions. Of these *Hyeria*, *Calamophyton*, *Aneurophyton*, and *Cladoxylon* present highly



FIG. 83 bis.

Hornea Lignieri. Two well-preserved sporangia, Sm^1 and Sm^2 , cut in accurate longitudinal section, terminating two slender stems. The sporangium below is bifurcate, that above simple. Note the columella in each, overarched by the spore-bearing-layer. $\times 12$. (From Scott, after Kidston and Lang.)

elaborated shoots, bearing appendages and numerous sporangia. They suggest a differentiated shoot, whether sterile or fertile, still in the making, as land-plants in an experimental stage. The same appears also from their internal structure, as suggested by such imperfect descriptions as can be drawn from material not too well preserved. For instance, in the large stems of *Cladoxylon* it has been possible to show that there is a plurality of vascular steles. Various large stems possessed a cambium ; this is seen particularly in *Aneurophyton germanicum*, where there is a solid central core of tracheidal primary xylem, three-lobed in transverse section, and it is immediately surrounded by a mass of secondary wood composed of radially arranged tracheides, traversed by deep medullary rays. At the present moment these fossils are doubtless suggestive enough as a basis of comparison. For their details reference should be made to special works on Palaeo-

phytology.¹ But the Psilophytales, as being the best preserved and also the simplest in general structure, will provide the best basis for morphological discussion.

The first impression conveyed by a review of the known Psilophytales is that they conform to one consistent type of organisation, and that a simple one. Hitherto these plants give no information as to the balance of the sexual and spore-bearing phases of the life-history, for their gametophytes are still unknown. The plants as here described are clearly sporophytes; but the development of spore-tetrads, similar to those of other Pteridophytes, points without doubt to the existence of some gametophyte stage. The absence of direct evidence suggests that the prothallus will have been relatively simple, and probably delicate in texture; but we are left to draw inferences from the sporophyte only.

Comparisons may be made on the one hand with the relatively simple Bryophytes, and on the other with the Vascular Vegetation of the land, where the form of the plant-body is often elaborate. The Psilophytales differ broadly from the former in the physiological independence of the sporophyte, as an organism fixed though not technically rooted in the soil; in the continued apical growth and branching, in the presence of leaf-like organs in some of them, and in the plurality of their distal sporangia; also in the presence of vascular tissue, though this is of a rudimentary type. They share with some of them a photosynthetic system, but it is comparable with that of the Anthocerotales rather than with any other Bryophyte type. On the other hand their morphological organisation as a whole stands on a lower plane than that of most living Pteridophytes. These present relatively few main types of organisation, such as Ferns, Equiseta, Lycopods, and Psilotales. In them the vegetative parts of the sporophyte fall mostly into recognised categories of stem, leaf, and root, a classification which applies to land-plants generally, and owes its origin and universality to requirements common for all sub-aerial plants of fixed habit; in fact, for all such as have attained to full harmony with their surroundings. But in these early Devonian plants that harmony does not appear to have been fully established as is shown by the imperfect differentiation of the parts. We enquire which of the vascular plants now living show a similar imperfection, and there can be no doubt that it is most marked in the Psilotales. But comparative discussion will best be deferred till these and certain other primitive types of vascular plants shall have been described. In particular, the comparison of the underground parts will not be taken up till after the cognate facts for the Lycopodiales shall have been considered (Chapter XIV).

¹ For descriptions and figures of these reference should be made to the memoirs of Kräusel and Weyland. Also, for a general resumé, to Hirmer, *Handbuch d. Paläobotanik*, 1927; also to the later memoirs of Lang, *Trans. R.S.E. and Phil. Trans.*

CHAPTER VIII

PSILOTALES ¹

THE genera *Tmesipteris* and *Psilotum* are the only living representatives of this Class, and they are characterised by peculiar features which give them an isolated position among plants of the present day : these, however, they have in common, so that there is no doubt of the natural kinship of the two genera. Both are natives of Australasia, to which region *Tmesipteris* is restricted ; but *Psilotum* spreads through the Tropics, both east and west. *Tmesipteris* appears in various modifications ; by some botanists these are all regarded as referable to one species, *T. tannensis*, Bernh. Latterly, however, while this designation is retained as including the epiphytic and pendulous types, a long-established variety which is erect and of ground-growing habit has been recognised as a distinct species, viz., *T. Vieillardii*, Dang. The genus *Psilotum* comprises two species, viz., *P. triquetrum*, Sw., which is an upright shrub with triquetrous branches, and *P. complanatum*, Sw. (incl. *P. flaccidum*, Wall), which is pendulous with flattened branches. These plants are all rootless ; in place of roots they have leafless and forking rhizomes, from which aerial shoots arise, more or less freely dichotomous, bearing leaves and sporangiophores. Their nutrition is partly saprophytic with mycorrhiza, partly photosynthetic. The latter function is centred in the green distal part, which takes the form of a lax shoot not clearly differentiated into nutritive and propagative regions.

In *Tmesipteris* the structure is in some respects simpler than in *Psilotum*. The habit is peculiar, the plant being usually established on the trunks of

¹ *Selected Literature on the Psilotaes* : C. E. G. Bertrand, *Arch. Bot. du Nord*, Paris, 1881, p. 467. Solms Laubach, *Ann. Jard. Bot. Buitenzorg*, vol. iv., 1884, p. 174. Dangeard, *Comptes Rend.*, 1888, and *Le Botaniste*, Caen, 1890-91. Bower, "Studies, I.," *Phil. Trans.*, 1894. Thomas, *Proc. Roy. Soc.*, vol. 69, 1902, p. 350. Pritzel, *Natürl. Pflanzenfam.*, i., 4, 1902, p. 606, where the older literature is fully quoted. Boodle, "Anat. Psil.," *Ann. of Bot.*, xviii., 1904, p. 505. Ford, *Ann. of Bot.*, xviii., 1904, p. 589. Sykes, *Ann. of Bot.*, xxii., 1908, pp. 63, 525. Stiles, "Psil. flaccidum," *Ann. of Bot.*, xxiv., 1910, p. 373. Darnell Smith, "Prothallus Psil.," *Trans. R.S. Edin.*, vol. lii., 1917, p. 79. Lawson, "Prothalli," *Trans. R. S. Edin.*, vol. li., p. 787, and lii., p. 93, 1917. Holloway, "Prothalli and Embryos," *Trans. N.Z. Inst.*, vol. 1., 1917, p. 1 : and liii., 1921, p. 386. Bower, "Primitive Spindle," *Proc. R.S. Edin.*, 1922. Campbell, *Mosses and Ferns*, 3rd edn., 1918, pp. 504 ; here the literature is fully cited. Sahni, "Tmes. Vieillardii," *Phil. Trans.*, B. vol., 1925, 213, p. 143. Zimmermann, "Stomata," *Zeitschr. f. Botanik.*, Bd. 19, 1926, p. 129. C. I. Meyer, "Sporangia," *Jard. Bot. d. Moscou*, 1927, p. 62. Von Goebel, *Organographie*, iii. Aufl., Teil ii., 1930, *passim*.

tree-ferns; though occasionally it is of a ground habit, as in the New Caledonian type now distinguished as *T. Vieillardii*. The rhizome, which

fixes it in the substratum, is repeatedly branched in a dichotomous manner, and is without appendages other than rhizoids. Strong branches of this system curve upwards or outwards towards the light, and develop as the aerial shoots. These are usually unbranched though occasionally a dichotomy may be observed (Fig. 84, *A*). The aerial shoots differ from the rhizomes in bearing appendages: at first small scale-like bodies are produced externally; but higher up successively larger leaves are produced till the condition of the fully formed "foliage leaf" is attained; each of these is about half an inch long, and flattened in a vertical plane, with a "mucronate" tip. This basal vegetative tract is continued directly into the fertile region, the distinctive feature of which is that forked branches, or fertile twigs, appear to take the places of the simple foliage leaves. Each fertile twig consists of a stalk bearing two leaf-lobes similar in form to the sterile leaves, and between them is a synangium with two large and confluent antero-posterior sporangia (Fig. 84, *B*, *C*, *D*). The arrangement of the appendages on the mature axis is irregularly alternate, and this appears in the transverse section of an apical bud (Fig. 85).

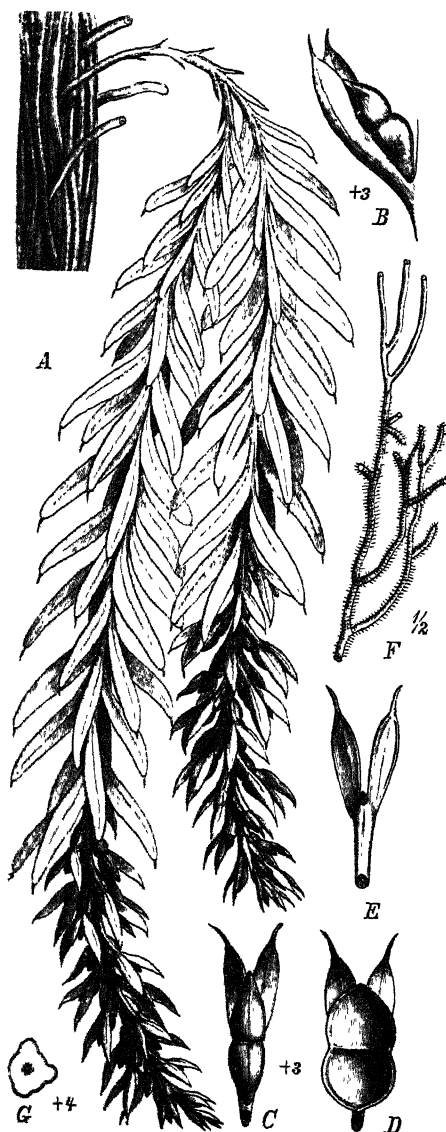


FIG. 84.

Tmesipteris lannensis, Bernh. *A* = Habit-figure of a whole plant (pendent form), showing a dichotomy. Natural size. *B-E*, fertile twigs, with synangia; *B*, seen from the side; *C*, from above; *D*, after dehiscence; *E*, from the under (dorsal) side, all \times about 3. *F* = rhizome $\frac{1}{2}$ natural size. *G* = transverse section of old stem, \times 4. (After Pritzel in Engler and Prantl, *Nat. Pflanzenfam.*)

The central axis is irregular in section owing to the projection of the decurrent bases of the appendages, which are borne alternately upon it; in this case three fertile branches (*l-sy-l*) are inserted below two sterile leaves (*f*); but the succession is as a rule irregular. The fertile region forms a very lax strobilus, in which the following features may be noticed. It does not differ markedly from the vegetative region in the size of the parts which it bears: it is not composed exclusively of fertile branches, but foliage leaves of the usual type may be interspersed among them; not uncommonly there is reversion from the fertile back to the vegetative state. In fact, as regards the sterile and fertile appendages the condition is the same as that in the "*Selago*" section of *Lycopodium* with its successive sterile and fertile zones.

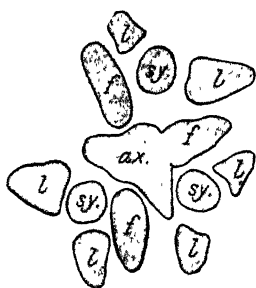


FIG 85.

Transverse section through a sporangiferous bud of *Tmesipteris*. *ax*=axis. *f*=foliage leaves. *l*=lateral lobes. *sy*=synangia. $\times 20$.

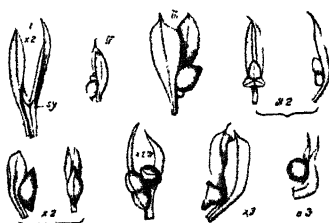


FIG 86.

Tmesipteris tannensis, various unusual forms of fertile twigs; in *i* the synangium is abortive; in *ii* and *iii* one loculus is abortive; others show a larger number of loculi than two; others again, right and left on the lower row, show a single loculus, the septum being imperfect, or absent.

Not uncommonly the fertile twigs of *Tmesipteris* show deviations from the normal as thus described, and particularly about the limits or about the middle of the fertile zones. Near to the lower and especially about the upper limit of fertility variations of reduction from the normal may be found, showing abortion of either loculus of the synangium, or of both of them (Fig. 86, *i*, *ii*, *iii*), or the two loculi may be imperfectly formed, the septum being incomplete, and the synangium is thus replaced by a single loculus (Fig. 86, lower row). These suggest deficient nutrition. Conversely, about the middle of the fertile zone, where nutrition is presumably most efficient, certain twigs may be developed beyond the normal. There may be an additional loculus (Fig. 86, top, right). But not unfrequently repeated dichotomy of a twig may be found, with two or even three normally shaped synangia, one at each fork; moreover, the synangium is not always sessile, but may be raised on a longer or shorter stalk; it may even be replaced by a leaf-lobe similar to the normal type. The theoretical bearings of such variants as these, which have been recorded by several observers, and do not appear to be uncommon, will be discussed later (Chapter XXVII).

In *Psilotum* the main features resemble those in *Tmesipteris*, but with differences of detail. The underground rhizomes are rootless and leafless,

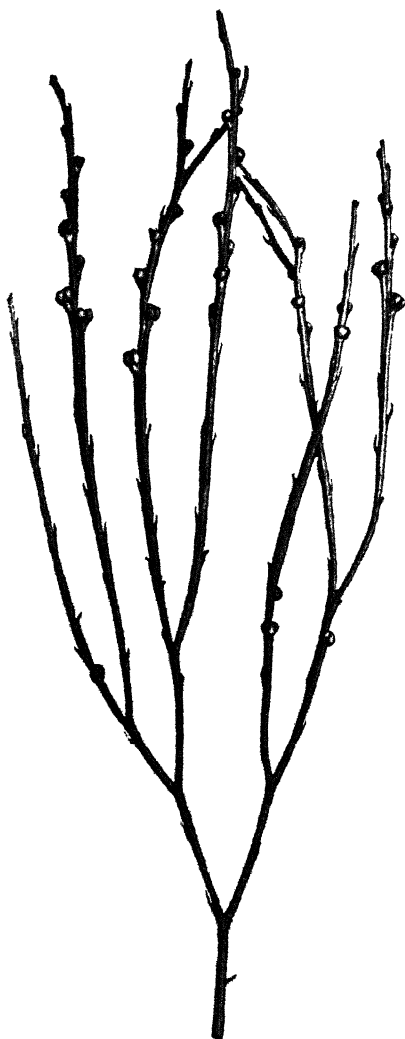


FIG. 87.

Psilotum triquetrum, Sw. Shoot showing repeated dichotomy, bearing minute tooth-like sterile leaves, and turgid synangia attached to the minute fertile twigs. It is to be noted that a sterile region intervenes between two fertile regions. Natural size.

as in *Tmesipteris*, but are more profusely bifurcate; they bear rhizoids and show mycorrhiza. They occasionally produce gemmae, which freely propagate the plant vegetatively. The aerial shoots bifurcate much more freely than in *Tmesipteris*, in planes successively at right angles (Fig. 87). Following on a basal region which has no appendages the aerial shoot bears minute vegetative leaves, but without constant or definite arrangement. Those first to appear are small subulate processes, arising from the projecting angles of the green axis, and they are without vascular tissue (Bertrand, *l.c.*, p. 455). In the upper regions of strong shoots they are replaced by fertile branches or twigs, of the same type as those of *Tmesipteris*, though much smaller. Each consists of a very short stalk, bearing two minute subulate leaves, right and left, and between them a sessile synangium with normally three loculi (Fig. 87). Here, as in *Tmesipteris*, there is no definite strobilus: the fertile shoot is very lax, while the minute sterile leaves are interspersed irregularly between the fertile twigs. There is thus a "Selago" condition which is even more obvious here than in *Tmesipteris*.

Psilotum, like *Tmesipteris*, is also open to deviations of structure of the fertile parts. Reduction of the sporangia from the normal three to two is not uncommon, but often it is seemingly due to arrest of one of the loculi. In other cases the number may be increased to four or five. There are also

fairly numerous instances recorded for *Psilotum* of accessory forkings of the fertile twig, resulting in specific cases in two synangia and three very minute leaves, or in three synangia and four leaves; the parts are then crowded together, and more or less fused. Already in 1902 Thomas drew as an inference from such facts that the repeated dichotomy is an ancient feature (*Proc. Roy. Soc.*, vol. 69, p. 350). More recent comparisons tend to uphold that view.

ANATOMY

The internal structure of the Psilotales is relatively simple, in accordance with their outward form. It is comparable with that of the Psilophytales, but more definite. The axis is traversed by a stele which is of the protostelic type: it is limited externally by an endodermal sheath which is more definite in *Psilotum* than in *Tmesipteris*.

The broad cortex of the aerial shoot is surrounded by a well-marked epidermis with numerous stomata, and superficial hairs are absent; in the rhizome it is less definite, and rhizoids are present. The epidermis of a stout aerial stem of *Psilotum* consists of elongated cells with greatly thickened external walls, while the inner walls are thin; the stomata are slightly depressed. They are of an archaic type, with

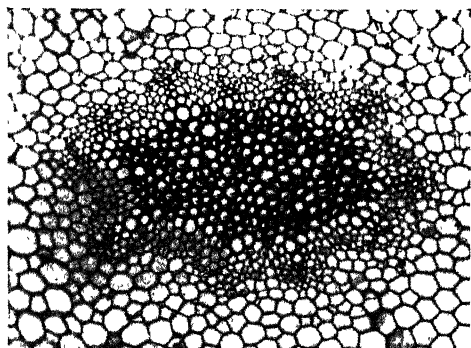


FIG. 88.

Transverse section of the stele of a large and apparently leafless stem of *Psilotum*, showing ten distinct xylem rays: the central tissue is sclerotic. (After a photograph by Gwynne-Vaughan.)

two dumb-bell-shaped guard-cells, the walls being lignified after the manner of Gymnosperms. They closely resemble those of *Tmesipteris Vieillardii*, and of *Rhynia*; but those of *Asteroxylon* are of a more specialised type (Zimmermann, *Zeitschr. für Bot.*, 1926). The massive cortical tissue of the aerial shoot in *Psilotum* is differentiated into three zones: the outermost is the chief photosynthetic tissue of the plant, consisting of thin-walled cells with large intercellular spaces (Fig. 91 *bis*, *b*): a middle zone is composed of four to five layers of indurated mechanical cells, and there is an inner band of thin-walled cells limited internally by the endodermis. The cortex in the rhizome is not so differentiated; it consists of thin-walled starchy parenchyma with endophytic mycorrhiza.

The structure of the stele is of the type described as radial (Fig. 88). Starting from the smaller branches of the rhizome of *Psilotum*, and passing

upwards to those of larger size, and finally along the aerial shoot, the protosteles is continuous, but subject to structural changes as it enlarges conically

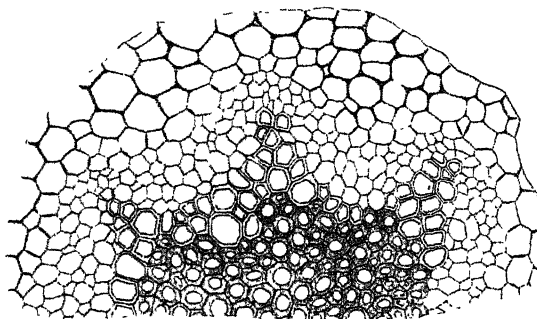


FIG. 89.

Psilotum triquetrum. Part of a transverse section of the central stele. $\times 100$.

upwards. It is throughout bounded externally by endodermis, and consists at first of a central tracheidal tract surrounded by phloem and conjunctive parenchyma. In the smallest rhizomes, where the stele is minute, this



FIG. 90.

Diagram illustrating the organisation of the shoot of *Tmes. Veillardii*. The xylem is black: pith and inner cortex white: leaves and their decurrent bases dotted. (After Sahni.)

tracheidal tract is of cylindrical form; it increases in proportion to the size of the part, showing gradual steps of moulding and even of disintegration upwards. The result is a stellate section of the woody tract, with projecting flanges of protoxylem varying in number roughly according to size (Bertrand, *l.c.*, Figs. 134-162). A central pith also appears with an irregular outline, and isolated groups of tracheides may be detached owing to parenchymatous intrusion between the elements of the xylem. In the aerial shoots the central tissue is usually sclerotic, and with increasing size the number of distinct xylic rays may rise as high as ten (Fig. 88). The detail of structure of an average stele of *Psilotum* is shown in Fig. 89. An examination of the lower parts of the aerial shoot in *Psilotum* sometimes suggests a secondary formation of xylem; there is no definite cambium, though the additional tracheides show signs of radial arrangement. The secondary development fades

off upwards; this has its interest for comparison with *Sphenophyllum*, and certain other Pteridophytes in which secondary thickening is a marked

feature. In the stem of *Tmesipteris* also traces of secondary tracheides have been found, but they are feeble.

The rhizome of *Tmesipteris* exhibits much the same structure as that of *Psilotum*; there is at first a solid core of tracheides surrounded by phloem, with well-formed sieve-tubes of the Pteridophyte type, and an ill-defined endodermis (Sahni, *l.c.*, 1925). Often there is no distinct protoxylem, but as the passage is made to the aerial stem protoxylem appears, its position being mesarch. As the stele passes upwards and enlarges it becomes medullated.

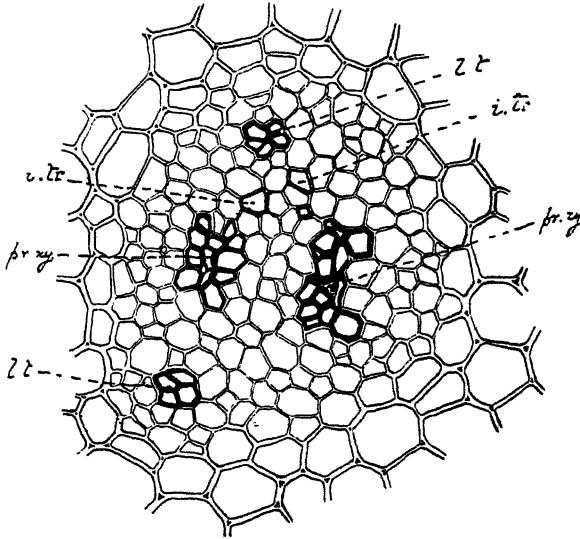


FIG. 91.

Tmesipteris tannensis. Transverse section of the sterile region, high up. The protoxylem (*pr. xy.*) is mesarch. The xylem of the stele is fading out, and being replaced by parenchyma; three of the tracheides (*i. tr.*) show incomplete development; there is no longer a complete ring, *l. t.* leaf-trace bundles. There is no definite endodermis. $\times 150$.

The structural transition has been followed by Sahni in *T. Vieillardii*, a ground-growing species from New Caledonia, with shrubby habit and narrow leaves (Fig. 90). As the stele expands and the pith appears certain strands of cauline tracheides remain traversing the pith longitudinally. These are held to be an archaic feature. Meanwhile the peripheral xylem becomes disintegrated into a ring of separate strands, a state arrived at also in the distal region of *T. tannensis* (Fig. 91). The relation of the stele to the large leaves of *T. Vieillardii*, and to the fertile twigs also, presents various features of interest. On passing from the rhizome to the aerial shoot there is a long transitional region with numerous scale-leaves. Most of these have traces which are merely strands of thin-walled cells, and they resemble the leaf-traces of *Asteroxylon* in that they stop short at the leaf-base, never entering the blade. Only in the leaves with a definite lamina does the bundle actually enter the free portion of the leaf, and even then it never penetrates to the distal tip. This is a more advanced structure than in *Psilotum*, and the difference is in accord with the larger size

of the leaves of *Tmesipteris*. The question has often been discussed of the relation of the off-coming traces to the xyletic gaps of the stele in *Tmesipteris*. Following on the observations of Sykes (*Ann. of Bot.*, vol. xxi., p. 86), the details have been examined by Sahni in *T. vieillardii*, with the result that the great majority of the gaps in the stele have no constant relation to any leaf-trace; they must therefore be regarded merely as xyletic perforations. This is what might have been expected, particularly in the distal region where the

vascular development is waning. It accords with what is actually seen there in *T. tannensis* (Fig. 91). The structure described and illustrated in Fig. 90, though within the limits of the conical stele, has its analogy with the vascular skeleton of those solenostelic Ferns which possess medullary tracts. But the dimensions here are smaller, ranging from a diameter of about 0.5 mm. (Sahni, *l.c.*, Text-Fig. 2 e), to about 1.0 mm. (*idem.*, Pl. 5, Fig. 13). Thus they fall below the size of 1.0 mm., about which diameter the incidence of solenostely becomes critical for Leptosporangiate Ferns (*Size and Form*, p. 121). In both cases the structural progression is shown in steles enlarging upwards, a relation that will be discussed in Chapters XVII and XXVIII.

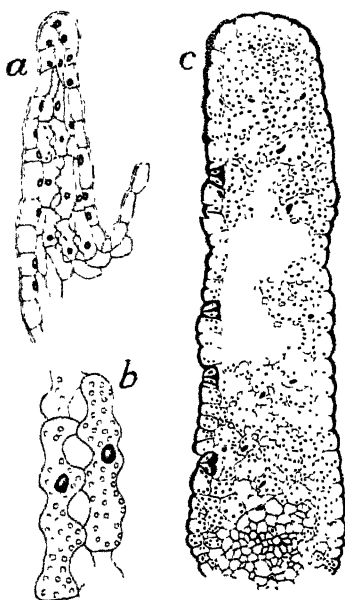


FIG. 91 bis.

Leaves of the Psilotaceae. (a) a leaf of *Psilotum triquetrum* in longitudinal section, showing epidermis without stomata, covering a well-ventilated mesophyll. $\times 26$. (b) cells of the cortex, of like structure. $\times 100$. (c) part of a transverse section of the laterally compressed blade *Tmesipteris*, showing epidermis with stomata only on one side, and well-ventilated mesophyll. $\times 52$. (a, b, after Ford; c, after Sykes.)

the photosynthetic cortex (Fig. 91 bis, a). The earliest scale-leaves of *Tmesipteris* have a similar structure; but as they pass on by gradual transition to the larger, laterally compressed leaves these adopt a more elaborate structure. Normal stomata may be present on both faces, while the mesophyll is so well ventilated as to give its cells a lobed appearance. A single vascular strand, running up almost vertically through the cortex of the stem, traverses the centre of these larger leaves, but it stops short just below the mucronate tip (Fig. 91 bis, c). The "mucro" appears structurally like one of the earliest scale leaves, as though it had been carried up bodily on a basal innovation. The fertile twig, with its two

The conical scale-leaves that appear on the aerial shoots of *Psilotum* have a very simple structure. Each is covered by a layer of epidermis with a thick cuticle, but there are no stomata. Within is a well-ventilated parenchyma continuous with that of

leaves and synangium, differs not only in its more elaborate form, but also in the fact that a more fully developed vascular strand enters the stalk, while a tracheidal tract passes up into the synangium. These structural facts will be considered comparatively later (see Chapter XXVII).

SPORE-PRODUCING PARTS

The apical cone of *Tmesipteris* is variable in bulk ; in strong shoots it may be a broad dome, while in weaker specimens, or in those in which the growth is beginning to fail, it may be comparatively narrow. A single conical cell is frequently present at the tip, but its segmentation does not appear to be strictly regular, and it is difficult to refer the whole meristem to the activity of one parent cell. Passing from the actual apex the sides of the cone are covered by deep prismatic cells, which are somewhat irregular in origin, depth, and arrangement. When a leaf or a fertile twig is about to be formed certain of these increase in size, and undergo periclinal and anticlinal divisions so as to form a massive growth, the summit of which is occupied by a single cell of wedge-like or prismatic form. In these early stages it is impossible to say whether the part in question will be a vegetative leaf or a fertile twig, so similar are they in their initial stages. Those, however, which are to develop as fertile twigs soon show greater bulk : while they grow less in length, a swelling appears upon the obliquely adaxial face (Fig. 92, *A*). The superficial cells involved in this undergo more or less regular divisions, a band of tissue four or more layers in depth is thus produced. In this two masses of internal cells assume the character of sporogenous tissue, while the whole swelling begins to adopt the two-lobed form of the synangium (Fig. 92 *B*). Though the two sporangia thus begin to take form, it is exceedingly difficult to define the actual limits of the sporogenous mass which each contains. The more superficial tissues, as well as the band of cells intervening between the two sporogenous masses remain sterile, the former developing into the walls of the synangium, the latter into the septum. Meanwhile the two leaf-lobes enlarge right and left, and the hump on the abaxial side of the fertile twig as seen in median section (*B*) represents a sort of commissure between them. Already a procambial strand is seen traversing the stalk (Fig. 92, *B*, *vb*). The vascular strand thus initiated extends into the mature twig ; it gives off branches right and left to the leaves, and entering the stalk of the synangium gives off strands, again right and left, which traverse the margins of the septum (Fig. 92, *C*). It ends in a small process in a median position between them, which has been regarded as " representing the vascular supply of the apex of the branch " (Sykes).

In radial sections of the terminal bud of *Psilotum* the fertile twigs present a general outline and structure as in *Tmesipteris* ; but naturally only one of the three sporangia of a synangium can be cut exactly in median section, and according to their orientation relative to the main axis that sporangium

must be the obliquely abaxial one. Fig. 93, *A*, shows a young fertile twig as a whole. The cell marked (x) may represent an initial cell, though it is difficult to refer the whole structure to successive cleavages from it; moreover, other observers have held the synangium as terminal. Already the

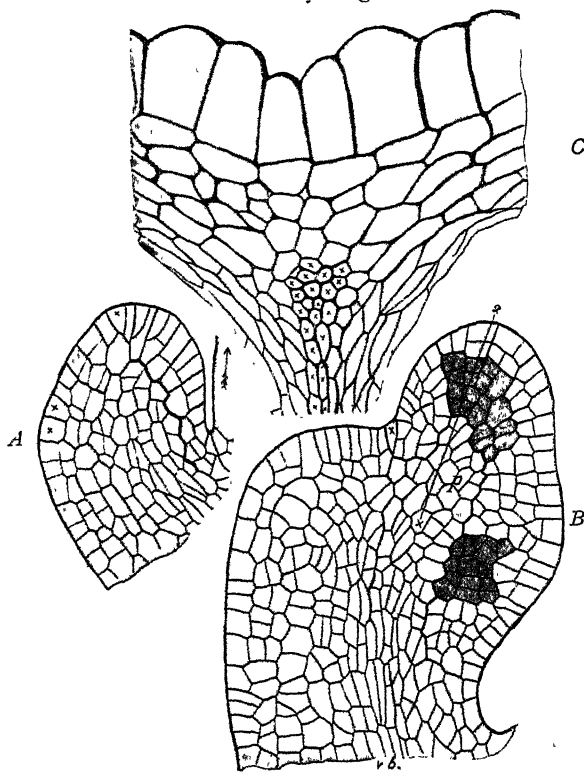


FIG. 92.

Tmesipteris tannensis. *A*—very young synangium arising from the adaxial surface of the fertile twig. $\times 100$. *B*—a fertile twig bearing a much older synangium; the sporogenous masses are shaded. $\times 100$. *C*—part of a radial section of a mature synangium showing the insertion of the septum. $\times 100$.

synangium can be recognised as a bulky projection directed obliquely towards the main axis, as indicated by the arrow. Fig. 93, *B*, *C*, *D*, are sections of successively older synangia, omitting the rest of the fertile twig. All of them have the same orientation, as indicated by the arrows, and each has traversed the abaxial loculus in a median plane. The shaded tracts are believed to indicate the sporogenous tissue, and suggest its reference in each loculus to a single archesporial cell; but this point is not insisted upon.¹ The same

¹ The question is really immaterial, but it may be pointed out that C. I. Meyers drawings, Nos. 3, 4, 6, cannot be held as valid proof of the contrary, since each represents *two* loculi out of the three; hence the plane of section through any one individual loculus cannot possibly have been median. (C. I. Meyer, *Jard. Bot. Université Moscou*, Sept. 30, 1927, pp. 52-64.)

difficulty in recognising the limits of the sporogenous masses arises here as in *Tmesipteris*. In the subsequent stages, as seen in Fig. 93, *C*, *D*, *E*, the sporogenous masses assume large dimensions, and are at first composed of uniform cells. The wall of the synangium meanwhile becomes multiseriate,

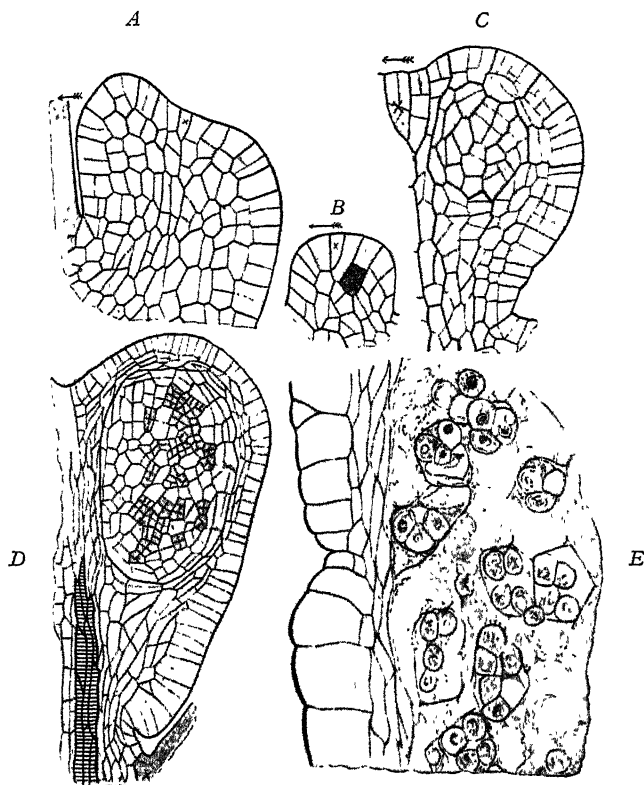


FIG 93.

Psilotum triquetrum, Sw. Various stages of development of the fertile twig and synangium. In *C* the sporogenous group is shaded. *D* shows the differentiation of its cells, the fertile cells being shaded. *E* shows the disorganisation of the remaining cells without forming spores. $\times 100$.

and the cells of the outermost layer take a deep prismatic form, while the inner layers are shallow. The same is the character of the more superficial cells of the sporogenous mass (Fig. 93, *D*), so that it is almost impossible to recognise the limit between the tissue of the wall and of the sporogenous mass. The superficial portions of the latter become disorganised without the formation of spores, but there is no clearly defined tapetum. Such is also the fate of a considerable proportion of the more central cells; for, as the synangium develops, irregular groups of cells of the sporogenous masses assume dense granular contents and subdivide, while the rest remain paler, with more

watery contents, and do not divide. The products of the former undergo the final tetrad-division and form spores, while the others become disorganised. The actual state of partial disorganisation is seen in Fig. 93, *E*. Thus a sterilisation of cells of the sporogenous tissue occurs in *Psilotum*; the same appears also in *Tmesipteris*: it will be seen later that the like occurs also in *Equisetum*.

In both genera of the Psilotaceae the lines of dehiscence of the mature sporangia are defined structurally. In *Psilotum* those lines radiate from the centre of the synangium, and the same holds also in *Sphenophyllum majus*. It remains to be seen how far there is correspondence between these plants in respect of other features. The spores are usually of the bilateral type, like the microspores of *Isoetes*; but some of them may also be found to be of the tetrahedral type. In this a comparison may be drawn with the Schizaeaceae.

THE PROTHALLUS AND THE EMBRYO

The Psilotales have been the last Class of the Pteridophyta to yield up the facts relating to their gametophyte and embryogeny. Not till 1917 was there any certain knowledge of these, but in that year Darnell-Smith succeeded in germinating the spores of *Psilotum* experimentally and found the fungal infection to be initiated as early as in the third cell formed. Lawson described its prothallus in some detail. Later he followed this up by a like description for *Tmesipteris*, but it remained for Holloway in 1918 and 1921 to give a full account not only of the prothallus but also of the embryogeny of *Tmesipteris*. Unfortunately the embryo of *Psilotum* remains still to be described, but enough is now known of the gametophyte and sexual reproduction in this Class to provide a basis for important comparisons.

The prothallus in both genera is subterranean, of light brown colour, and roughly of cylindrical form, with an obconical base where it sprang from the germinating spore. It branches irregularly, each branch having an active growing point. It is devoid of chlorophyll, and completely saprophytic, through co-operation with an endophytic fungus, which is not strictly localised; but the growing points and sexual organs are not invaded. Rhizoids are distributed irregularly over its surface, as are also the antheridia and archegonia. The prothalli are hermaphrodite; the appearance of that of *Psilotum* is as in Fig. 94, *A*, while the transverse section (*B*) shows the irregular distribution of the fungal infection, and of the antheridia and archegonia on the cylindrical thallus. The antheridia are hemispherical and project from the surface; they are unusually large, those of *Tmesipteris* being about twice the size of those of *Psilotum*, the male gametes are coiled and multiciliate bodies. The archegonia are constructed on the plan usual for

Pteridophytes, the venter being partially sunk, while the neck, composed of four rows of about six cells each, projects. After fertilisation the lowest tier of cells remains persistent, while the rest of the neck is deciduous. Unfortunately Lawson, to whom we owe these data, was unable to make more than isolated observations on the embryology of either genus. His drawing of a slightly advanced embryo of *Tmesipteris* presented a problem of embryology rather than a solution, so long as a complete account was still wanting (Fig. 95). The above description is based on the observations of Lawson

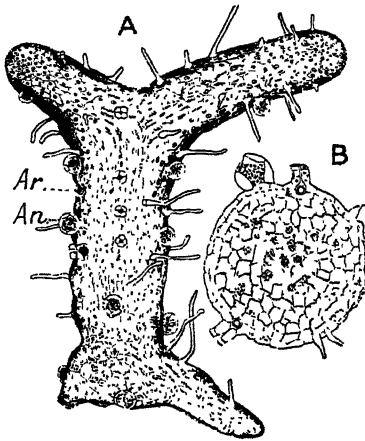


FIG. 94.

Prothallus of *Psilotum*. A.—the whole of a young specimen with an active apex to each branch. Laterally rhizoids, antheridia and archegonia ($\times 18$). B—transverse section, showing endophytic fungus, rhizoids and sexual organs ($\times 25$). (After Lawson.)

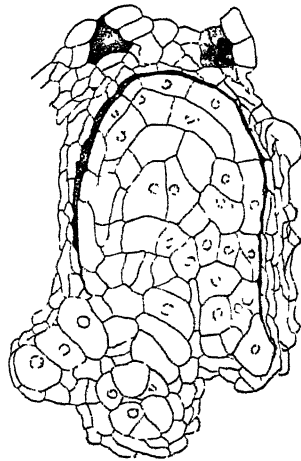


FIG. 95.

Tmesipteris. Section through a portion of a prothallus containing an embryo, with its haustorial base. Two effete archegonia lie above its apex. (After Lawson.)

(*Trans. R.S. Edin.*, 1917). A more consecutive story, based upon ample material obtained in New Zealand, has been given by Holloway for *Tmesipteris* (*Trans. N.Z. Inst.*, 1918-1921). Its interest fully justifies a full abstract; indeed, the embryology of this plant is in itself the most important contribution to that branch of morphology made in recent years. A similar account of the embryology of *Psilotum* would be equally welcome.

The spores of *Tmesipteris*, germinating deep-seated in the soil, give rise to prothalli of conical form, which never seem to reach the light; they are mycorrhizic from the first. This was found by Darnell-Smith and by Lawson to be the same in *Psilotum*. With the fungal infection goes a brown colour, which, however, fades off towards the apical region, where the tissue is not invaded by hyphae and consists of parenchyma often stored with starch. The tip is occupied by a meristem which possesses active apical growth, but the segmentation appears to follow no definite rule. Many rhizoids are

present (Fig. 96, *A*). Sooner or later the prothallus forks dichotomously, but the branches rarely develop equally. The specimen shown in Fig. 96, *B*,

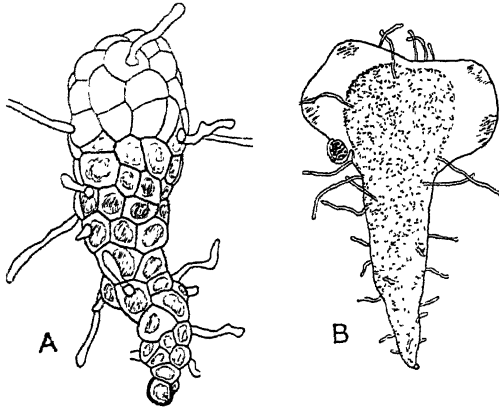


FIG. 96.

Young prothalli of *Tmesipteris*, after Holloway. *A* = very young stage, showing origin from spore, and fungal infection. $\times 55$. *B*. Prothallus of medium age, showing conical form and distal forking. The fungal area is dotted. $\times 18$.

has forked twice, and its form is unusually symmetrical; the drawing also shows the limits of the fungal distribution. As a rule the form of the adult prothallus is indefinite: an example is seen in Fig. 97, *A*. Bulbils are

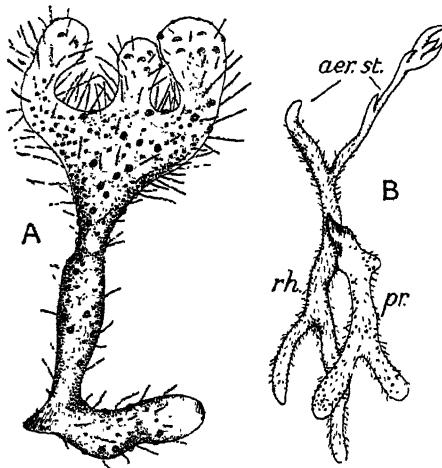


FIG. 97.

Complete branched prothalli of *Tmesipteris*. *A*, shows one main branch with further irregular branching. The objects borne on the three distal lobes are antheridia. $\times 5$. *B*, a large prothallus bearing a young plant, with both rhizome and aerial stem. $\times 1\frac{1}{2}$. (After Holloway.)

occasionally borne laterally, like those described by Solms for the sporophyte of *Psilotum*. There is no differentiation of the prothallus of *Tmesipteris* into

vegetative and reproductive regions, such as is frequent in subterranean prothalli. The sexual organs are distributed in large numbers over its whole surface, and intermixed. The young stages are found immediately behind the apex, but they may also arise further back from it; in fact, there is no strict acropetal sequence, except towards the extreme tip. Nor is there any constant indication of dorsiventrality in their arrangement; as a rule they are distributed more or less evenly around the surface of the thallus. The antheridia, which are hemispherical in form and relatively large when mature, arise each from a single superficial cell, which divides periclinally. The outer cell forms a wall consisting of a single layer of cells, the inner gives rise to the numerous spermatocytes (Fig. 98). The archegonia are of the type usual for vascular plants, but they show a certain peculiarity of the neck. This is formed of four rows each consisting of four or five cells (Fig. 99). After the archegonium has matured the outer three or four tiers of neck-cells fall off, leaving behind the lowest tier whose walls become strongly cutinised and brown coloured.

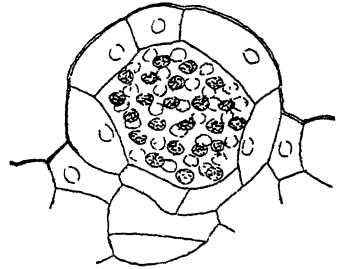


FIG. 98.
Mature antheridium of *Tmesipteris*. $\times 150$.
(After Holloway).

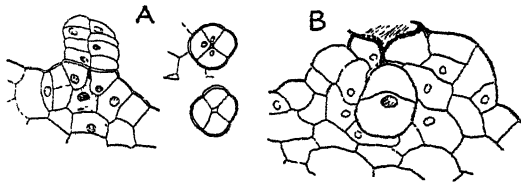


FIG. 99.
A = archegonium of *Tmesipteris*, after Holloway. \times circ. 100. B = fertilised archegonium after the projecting neck has been shed, and the first cleavage of the zygote. \times circ. 100.

This behaviour in *Tmesipteris* is found also in *Psilotum*; it is unusual among Pteridophytes, though not unique. Bruchmann has described how in the ripe archegonium of *Lycopodium complanatum* the upper tiers of neck-cells are thrown off "durch Abstossen" (*Bot. Zeit.*, 1908, p. 178). The interest in this is enhanced by the fact that in the Anthocerotales also the four distal "cover-cells" of the archegonial neck are thrown off. The parent-cell of this outer rosette appears to be the correlative of that outer cell which in the Psilotales gives rise to the four rows of the neck. In *Anthoceros* it is quartered as in the Psilotales, but there is no further division, and the group are detached before fertilisation (Campbell, *Mosses and Ferns*, 2nd ed., pp. 134, 151). In the Psilotales, however, the products of the correlative cells are thrown off after fertilisation, excepting the basal tier. Notwithstanding these minor differences, this peculiar behaviour of the archegonial neck is

common to three very ancient stocks, viz., the Anthocerotales, Psilotales, and the Lycopodiales.

The embryology of *Tmesipteris* presents features of the greatest comparative interest.¹ *The leading fact is that the Psilotaceae give the first known example of a vascular plant in which the young sporophyte is rootless and leafless.* A single prothallus may produce a plurality of embryos, but in feeble prothalli these frequently do not progress beyond the initial stages. The first cleavage of the enlarging zygote is by a wall transverse to the axis of the archegonium; the hypobasal cell gives rise to the foot, and the epibasal to the shoot (Fig. 100, i). The succeeding cleavages appear to be

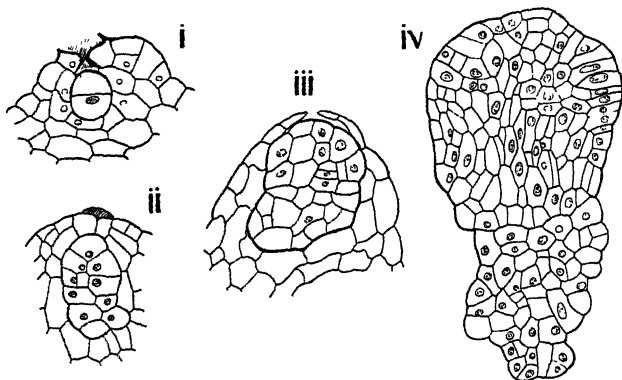


FIG. 100.

Embryos of *Tmesipteris*, after Holloway. \times circ. 75. They are all orientated with the axis of the archegonium vertical: but in nature it is variously inclined. For details see text.

rather irregular, sometimes with marked abnormalities. Holloway recognises an apical cell of the shoot set apart early in the epibasal hemisphere (ii), but it is difficult to trace any consistent scheme running through his numerous drawings. More decisive indications of apical growth with a single initial appear later, and frequently by number and position they indicate that early forking has taken place (iv). Meanwhile a median tract of elongated cells shows the origin of a conducting vascular strand, which forks upwards to supply the individual branches. The whole character of these early embryonic stages suggests an imperfect differentiation of parts, which in consideration of the adult structure may be held to be a relatively primitive rather than a reduced state of organisation. The hypobasal region gives rise only to the foot, which presents features of great interest: the outline of it becomes very irregular as the embryo advances in development (Fig. 100, iv). Outgrowths of individual cells or groups of cells result in haustorial processes variable in size and form (compare Fig. 95). The absorbing surface of the foot is thus enlarged. The thallus responds on its part by concentration

¹ Holloway, *Trans. N.Z. Inst.*, 1917-1921.

of nourishment in close contact with this centre of absorption (Fig. 101). But the activity of the foot is only temporary, though in some instances pro-



FIG. 101.

Base of the young sporophyte of *Tmesipteris* shown in Fig. 429, here cut in median section : the haustorial foot is seen below the basal wall, and starch accumulated in it. $\times 66$. (After Holloway.)

longed : sooner or later the young plant becomes detached at the basal wall, the whole foot remaining still embedded in the tissue of the prothallus ; the sporophyte is thus set free, though still retaining the scar of the previous attachment (Fig. 103, *ft*).

The epibasal region forms the shoot, but the irregularity of its development is in striking contrast to what is seen in most other Pteridophytes. The nearest approach to it may be found in some species of the genus *Lycopodium*. Sometimes a single apical meristem is formed, continuing the direct axis of the whole embryo. Young plants up to 4 mm. in length may frequently be found in which growth is taking place from only one apex ; *the whole plant is then a simple spindle* (Holloway, *l.c.*, Fig. 67). But more often apical growth may be initiated at a plurality of points, the most frequent being two, equally placed right and left in the epibasal region (Fig. 100, *iv*). Such branches may be unequally developed, while adventitious apices may also be formed at various points : in fact the young plants assume the most varied outline (Figs. 102, 103). The subterranean branches thus produced appear all alike, being cylindrical in form with radially projecting hairs. Where, as

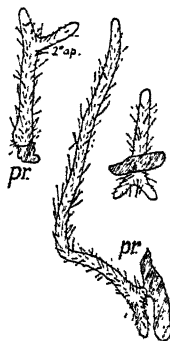


FIG. 102.

Young sporophytes of *Tmesipteris* of various form : the prothalli shaded. $\times 3$. (After Holloway.)

most often happens, there are two of them, the stronger apex turns upwards out of the soil, the other continuing to extend in the humus; but sometimes both may emerge (Fig. 103, *B*). The emergent aerial shoot is at first thinner than the rhizome, and leafless; but leafy outgrowths appear at about half an inch above the soil though only as scale leaves, and frequently the first of these leafy shoots only reaches a height of one or two inches, then withering.

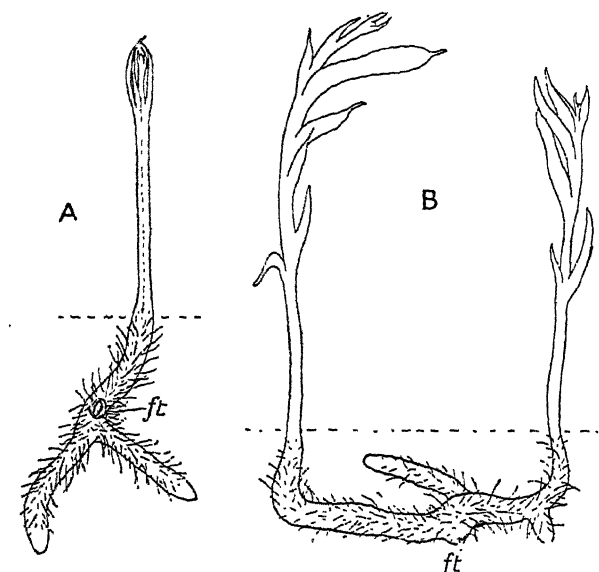


FIG. 103.

Young sporophytes of *Tmesipteris*. *A*, shows the first leafy shoot: *ft*=foot. *B*, has forked early, as shown by the position of the foot (*ft*), and both of the main apices have grown up into aerial shoots. $\times 3$. (After Holloway.)

The well-grown leafy shoots are only found when the rhizome-system has become strongly developed. They are then usually unbranched, but occasionally they fork, as already noted in the general description (Fig. 84). The scale leaves pass over into the fully-formed leaves, and finally the fertile region is reached.

COMPARISON

Comparative study of the Psilotales has presented problems of great difficulty to morphologists. One reason for this has been a persistent effort to assign the parts distinguished by the analysis of their sporophyte to the categories applicable for the majority of vascular plants of higher organisation than that which they present. Until quite recent times another difficulty has been the entire ignorance of their prothalli and embryogeny. A third has been the lack of living vascular types showing an organisation with which

theirs might be readily linked. In recent years, however, the discovery and detailed examination of important early fossils, and particularly those of the Devonian Period, has in great measure mitigated the third of these difficulties; while the almost simultaneous discovery of the gametophytes of both *Tmesipteris* and *Psilotum* has disposed of the second. The first is, however, a question of morphological method, which will now be more easily corrected since the field of comparison has been so greatly extended among vascular plants of relatively simple organisation. On the other hand, the organographic study of the Bryophytes at the hands of Professor Von Goebel has prepared the way for extending the comparison of the Bryophytes with the more archaic types of the Pteridophytes, across the gulf which had been held to separate the two simplest types of land vegetation. The comparisons will accordingly be no longer by preference with the more highly organised vascular plants, but with equal interest in both directions. Here the Psilotaes will, together with other early types, be regarded as organographic experiments caught on the evolutionary upgrade and left there: though modified, and perhaps condensed, so as to secure survival. It need no longer be assumed that their parts should fall into the definite categories laid down for plants of higher organisation. They will better be looked upon as essentially nascent, and probably all the more instructive from the incompleteness of that degree of differentiation which their parts have attained.

From this point of view the features of the Psilotaes may be considered comparatively, starting from the spore. The first steps of germination lead as a rule directly to a massive and obconical prothallus, somewhat after the manner of *Lycopodium cernuum* or *inundatum* (Fig. 96). Distally, as it grows on, the prothallus becomes cylindrical with irregularly branched extensions; but throughout its early construction it is radial. In this it resembles the prothallus of *L. phlegmaria*, and both of these are wholly saprophytic, a fact which may be related to the similarity in form. The genus *Lycopodium* teaches, through its variability of form and its instability as regards the mode of nutrition, that no great importance is to be attached to such comparisons, unless they are drawn along broad lines. In the plants here compared it may be held as significant that in them all the prothallus is at first conical and later cylindrical, the mycorrhizic and subterranean habits according with the latter form after the initially conical stage is past (Fig. 97). In all of these prothalli growth is localised at the apex, but there is no precise scheme of segmentation from one or more initial cells. Multiplication by bulbils is frequent in the Psilotaes, as it is also in *L. phlegmaria*. Mycorrhizic nutrition is a marked feature in both classes, as it is in so many of the ancient survivals. From these remarks it will be gathered that, beyond the underlying conical form and the radial construction, the prothalli of the Psilotaes do not provide distinctive material for comparison as regards their vegetative development.

The sexual organs of the Psilotales are clearly of the Pteridophyte type. The antheridia of either genus might perfectly well be those of some type of Fern, except for their large size, particularly seen in those of *Tmesipteris* (Fig. 98). The spirally coiled and multiciliate sperms accord with this comparison. The archegonia, which are much smaller, are also Fern-like, corresponding to a more advanced type, with projecting neck and only the venter sunk (Fig. 99). Their most interesting feature is the shedding of the distal tiers of the neck after fertilisation, while the cells of the basal tier, or in *Psilotum* sometimes two or more tiers, are retained and indurated. This appears to be exceptional among Archegoniate Plants, but a comparison may be drawn with the Anthocerotales, and occasionally with *Lycopodium* (see p. 137, small type).

The archegonia of the Psilotales project in all directions, with their axes at right angles to the surface of the cylindrical prothallus which bears them. Hence the orientation of the axis of the archegonium will be more or less indeterminate in relation to gravity. As usual the polarity of the embryo is defined by the first cleavage of the zygote, which is here transverse to the axis of the archegonium, hence it also is indeterminate in relation to gravity. Holloway's numerous drawings show the embryo of *Tmesipteris* as constantly *exoscopic*, that is, with its apex directed towards the neck of the archegonium (Fig. 100). This is its constant orientation in the Bryophyta, and it is the same in *Equisetum*. In most Pteridophytes, however, the embryo is *endoscopic*, or oblique. Whatever may be the bearing of this difference in orientation of the polarity of the embryo it appears that *Tmesipteris* shares it with the Bryophyta and not with the majority of the Pteridophyta.

The early character of the embryo of *Tmesipteris* is generalised rather than specific, and its features point to no known type of vascular embryology. There is no definite suspensor, nor is there any initial root or leaf. In fact, its features are chiefly negative. It has at first the form of a rather massive spindle attached by haustorial rhizoids to the prothallus. If a comparison be made between Lawson's drawing of a *Tmesipteris* embryo (Fig. 95) and a corresponding stage of the sporogonium of *Anthoceros* (Fig. 6, *E*), the similarity between them is clear. It may be that this similarity is due to no more than homoplastic reaction of relatively primitive plants of distinct affinity to like demands at the impressionable embryonic stage. But, on the other hand, these two archegoniate embryos share features which are collectively unique among primitive land-living plants. Instead of pressing the point of their similarity at this early stage of their development, it will be more instructive to enquire what follows in each as it passes to the adult state, and to note the steps by which they diverge. While doing so the end of spore-production common to them both must be borne in mind, together with the necessity for the nutrition of the spores during development.

Neither embryo at the stage compared shows any definite sign of what is to follow (Figs. 6 and 100). The hypobasal region in each is clearly haustorial; the epibasal consists of cells still undifferentiated. The alternatives open to the latter are either (i) direct spore-formation without branching or other marked morphological feature than intercalary growth, or apical growth soon arrested; or (ii) morphological elaboration with continued apical growth and branching, while spore-formation is deferred. The former is the method of the Bryophyta, with their capsules dependent on the gametophyte; the latter is the method of vascular plants with their independent sporophyte. The introduction of a basal intercalary growth, but without localised growth at the apex, gives the capsule of *Anthoceros* a means of producing a continued sequence of spores. However well this may be fitted for taking advantage of its prolonged dependence upon the gametophyte for the chief organic supply, it does not bear the promise of more than a limited success.

The second method, however imperfectly realised by such types as the Psilotales (or indeed the Psilophytales), bears at least the promising feature of localised and continued apical growth. When this is coupled with branching however ill coordinated, and with physiological independence however ill conceived in the actual plants of the Psilophytales or Psilotales as compared with the higher vascular plants, it contains the germ of unlimited further development. This is the suggestion conveyed by comparison of the young embryos of *Anthoceros* and of *Tmesipteris*, when considered in relation to their adult state. The question whether or not their obvious similarity is an index of phyletic relationship is a relatively minor point. The important difference lies in the localisation of apical growth. This, however, if unlimited, would be incompatible with prolonged physiological dependence.

The setting free of the young plant of *Tmesipteris* by shedding its connection with the hypobasal foot is the nearest approach yet attained by observation to the solution of the evolutionary problem inherent in the internal embryogeny of the Archegoniatae, viz., the establishment of a free vascular sporophyte on land. This example is not essentially unlike the separation of any Archegoniate from the parent prothallus. But here it occurs in organisms admittedly primitive, and it is carried out in a primitive way. For comparison with other Pteridophytes it is specially worthy of note that in *Tmesipteris* there is no sign of an enlarged protocorm. This is the more remarkable since both the prothallus and the young sporophyte are deeply involved in fungal symbiosis, which is so often accompanied by tuberous development.

It has been noted that in the apical growth of the young sporophyte of *Tmesipteris* there is no strict sequence of cell-cleavages. Frequently this apical growth is continued directly without any branching, so that it is not uncommon to find young sporophytes up to 4 mm. in length retaining a

simple spindle-form ; their vascular character is shown by a slender central tract of xylem. In fact, we here see a vascular sporeling of appreciable size without appendages, except rhizoids. When a branching of the young plant does occur it is not according to any set scheme. Though distal dichotomy is frequent the development of the limbs of the fork is usually unequal ; moreover, branching sometimes bears the signs of being adventitious. The resulting forms assumed by the young sporelings are very varied (Figs. 102, 103). This suggests that the plant is here more directly a creature of circumstances than is usual ; that it is essentially more or less amorphous, and that it has not settled down into any definite relation of its parts in the earlier phases of its development.

The embryogeny of *Tmesipteris* thus presents many points of special interest, most of which are negative. The usual question may be raised, whether its simplicity is to be held as primitive or as the result of reduction. The place which the Psilotales hold in general comparison, when based upon the adult state, makes the former view appear the more probable, in which case the nexus of the Anthocerotales, Psilophytales, and Psilotales seems to have been drawn closer by the discoveries of Lawson and of Holloway relating to the prothallus and embryo in the last-named Class.

In both genera of the Psilotales the transition from the leafless rhizome to the adult and fertile sub-aerial shoot is gradual (Fig. 84, *A*). The first appendages encountered on passing upwards are small ; larger leaves follow, till finally the region is reached where fertile twigs appear to replace these, or are intermixed with them. The disposition of these appendages upon the axis is somewhat irregularly alternate. With the added knowledge of cognate fossils, some of them leafless, and having before us the leafless embryology of *Tmesipteris*, the interpretation of their sub-aerial shoots becomes more intelligible than hitherto : for now the tendency will be to discuss them from the point of view of nascent organisation, rather than of reduction from some more highly organised source. There has been a tendency to neglect the detailed ontogeny of Psilotaceous leaves, and to concentrate upon the spore-producing parts. The chief problem has been to define the nature of the fertile twig—or “sporangienstand,” according to the nomenclature of Zimmermann. In the past two alternative views have been widely held ; either that the whole is of foliar-nature or that it is of shoot-nature. But a third view has also been suggested, that it is an organ or a group of organs *sui generis* : this may prove to convey present opinion better than either of the alternatives named. The developmental facts appear to be inconclusive in support of any of these views. Evidence based upon apical segmentation cannot be held as decisive, since in these plants it does not follow any precise scheme ; nor does the actual moulding of the parts when young give conclusive indications, since the parts appear to be almost simultaneous in origin, and rounded in form. Alternatively, an

opinion will need to rest upon a general comparison of the adult state, conducted in view of the probable relationship of the Psilotaes to other early vascular plants of the Land.¹

There is an underlying general similarity of organisation between *Asteroxylon* and the sporophyte of the living Psilotaes. This appears in the undifferentiated and branched underground rhizomes, in the gradual appearance of appendages of foliar nature (*Thursophyton*-leaves), as is seen on passing upwards along the sub-aerial shoots; and in the distal production of sporangia. In *Asteroxylon* there are in fact three successive zones of the plant body, all of them distinct, viz., the leafless rhizome, the leafy "*Thursophyton*-shoot," and the leafless "*Hostimella*-shoot." The general organisation of *Rhynia* and *Hornea* is similar, but without the *Thursophyton*-stage: this suggests that in *Asteroxylon* and the Psilotaes something has been super-added, a suggestion which agrees with the gradual appearance of the scale-leaves upon their upward-extending shoots. Comparison of the plants above named does not indicate that the scale-leaves are reduced structures, but rather suggests their *up-grade development*. The absence of any foliar development in the embryogeny of *Tmesipteris* is in itself an argument against reduction as accounting for their presence. If no other leafy plants were known to exist the ontogenetic story of *Asteroxylon*, or of *Psilotum* and *Tmesipteris*, would offer as the most direct and natural conclusion that a higher degree of organisation had been attained progressively by outgrowth of appendages not previously present, and that the method of their appearance was by *enation*, that is, as *outgrowths on a surface not previously tenanted, and laterally, not by distal dichotomy*. Enations are well known to exist sporadically on the shoots of certain plants of higher organisation. They appear there early, and are intermixed with other appendages, from which they are sometimes not readily distinguished in early stages. The difference between such lateral enation and distal branching may appear to be one of degree only, but the more primitive the organisation the clearer the distinction would be.

This whole question will be discussed later, when all the microphyllous types shall have been reviewed; for suggestions of a like nature may be made in the interpretation of them all (Chapter XXX). Meanwhile it is entertained as a working hypothesis for the elucidation of the Psilotaes and Psilophytales that the "*Thyrsophytoid*" scales arose by enation, and that their appearance was as new superficial outgrowths on the surface of parts already existent.

¹ Reference should be made to Solms Laubach, *Ann. Jard. Bot. Buit.*, iv., p. 139, where the literature up to 1884 is fully cited. Also to C. E. Bertrand, "Rech. s. l. Tmesipteridées," *Arch. Bot. du Nord.*, vol. i.; Bower, *Origin of a Land Flora*, 1908, chaps. xxviii., xxix.; Campbell, *Mosses and Ferns*, 3rd edn., with literature up to 1918; and to Zimmermann, *Phylogenie d. Pflanzen.*, 1930, pp. 124-126, where the literature up to date is fully cited.

It has been seen that in *Asteroxylon* the "*Thursophyton*" region, with its scale-like appendages, is phytographically distinct from the "*Hostimella*" region, which is without them. But there is no apparent cause which would preclude the formation of similar appendages on the "*Hostimella*" branches. As bearing on this we shall see later that while the fertile branches of certain microphyllous types bear sporangiophores only (*Equisetum*, *Archaeocalamites*), those of others not of distant affinity from them have sporangiophores and scales associated together (*Calamostachys*). In a type such as that of *Asteroxylon* we may then contemplate the possibility of the "*Thursophyton*" organisation invading the "*Hostimella*" region, and that scales should thus become associated with the spore-bearing organs. Further, that the latter, by condensation of branchlets each terminated in a sporangium would appear as the synangia, and that scale-leaves may have been associated with these with some degree of regularity. Such steps would provide an interpretation of the Psilotaceous strobilus more probable than either of those first suggested, and point to the third alternative. Each fertile twig (sporangiengstand) would then be a composite structure, consisting of a group of parts having different histories. The stalk would represent the base of a "*Hostimella*" twig—sometimes developed with supernumerary branchings, as is seen not infrequently in both genera of the Psilotaceae, especially towards the middle of a strobilus. The synangium with its varying number of sporangia would represent a corresponding number of ultimate branchlets condensed into synangial relation. The subtending leaves would be "*Thursophyton*" leaves, borne upon branches of the "*Hostimella*" region. The constancy in position of the subtending leaves to the synangium, as seen in the Psilotaceae, is probably the result of biological adjustment in relation to protection, nutrition, and perhaps also ventilation of the synangium.

Lastly, in comparing the small scale-leaves of *Psilotum* with the relatively large laterally compressed leaves of *Tmesipteris*, the difference is marked not only in form but also in elaboration of structure. The prevalent view from the time of Bertrand's memoir (*l.c.*, p. 455) has been that the former are reduced types of some more ample leaf. On the present working hypothesis they would appear to be nascent, and comparable with the scales of *Thursophyton* and other early fossils (Lang, *Phil. Trans.*, B. vol. 219, 1931). In that case how shall we regard the relatively large and complex leaf of *Tmesipteris*? Its distal apiculus or "mucro" has a structure like that of the scale-leaf of *Psilotum*; in both the leaf-trace stops short at its base, hence the "mucro" of *Tmesipteris* appears to represent the non-vascular scale-leaf of *Psilotum*. What then is the laterally flattened blade of *Tmesipteris* with its median vascular strand and photosynthetic equipment with numerous stomata? It may very probably be a zone intercalated as in so many Angiospermic leaves, carrying up on its tip the original scale-leaf, as they do the distal region of the leaf-primordium. A nearer comparison would, however,

be with the dermal appendages of the Cyatheaceæ and of *Gleichenia*, borne outwards on massive emergences (Fig. 252).

Our reading of the shoots of the modern Psilotales, in terms of advance rather than of reduction, would then be as follows: that *Psilotum* has advanced to the *Thyrsophyton*-state of the vegetative shoot; but *Tmesipteris* has produced in addition, as a photosynthetic amendment, a cladode-like intercalation of indeterminate character, which appears as its laterally-compressed blade. That in both of these genera the added appendages are continued as such from the vegetative to the fertile zone, which corresponds to the *Hostimella* region of *Asteroxylon* with its ultimate fertile twigs, which present very few branchings, condensed as synangia; but that these twigs are themselves associated with regularly disposed *Thyrsophyton*-appendages.

As thus advanced for a single group of microphyllous Pteridophytes the up-grade interpretation may appear somewhat open to criticism. Its more general application to other microphyllous types will provide a test of its strength or of its weakness. But meanwhile it should be borne in mind that this up-grade interpretation of the adult shoot of the living genera, and particularly of the fertile twig, accords with the facts of ontogeny, as revealed in the embryo of *Tmesipteris*; also with the anatomy as described by M. G. Sykes (*Ann. of Bot.*, xxii., 1908, p. 63), who had already reached a like conclusion without the aid of the embryological evidence.

CHAPTER IX

SPHENOPHYLLALES ¹

THE ancient and long extinct family of the Sphenophyllaceæ is represented according to present knowledge by the undivided genus *Sphenophyllum*: but associated more or less distinctly with it is the complex strobilus known as *Cheirostrobus*, and perhaps also the Noeggerathiae and Tingiae. As at present known they dated from the Calciferous Sandstone series of the Lower Carboniferous formation, and extended upwards to the Permian. They were plants of straggling habit, with the usual vegetative region preceding the spore-producing parts: these were commonly borne upon definite terminal strobili, but at least one case is known where the definition of the vegetative and reproductive regions was less clearly marked. In the case of *Cheirostrobus* the vegetative region is still unknown.

The vegetative system of *Sphenophyllum* consisted of a slender axis (Fig. 104), with elongated and fluted internodes intervening between successive superposed whorls of leaves, which in the cone, and sometimes in the vegetative region, were more or less webbed below. The branching of the shoot was irregular and monopodial: the branches were isolated and apparently axillary, though it seems uncertain sometimes whether they were not actually as in *Equisetum*, inserted between two of the whorled leaves rather than in the axil of one.

The leaves in each whorl numbered, as a rule, some multiple of three, six being a frequent number, though as many as twelve, or even eighteen, may be found in some species. They were commonly wedge-shaped, and more or less forked in the venation, with very various cutting extending more or less deeply

¹ *Selected Literature for the Sphenophyllales*: Williamson, "Organisation of Fossil Plants of the Coal Measures—Part V., *Phil. Trans.*, vol. clxiii., 1874, p. 41. Zeiller, "L'Appareil Fruct. d. *Sphénophyllum*," *Mém. Soc. Geol. de France*, No. ii., Paris, 1893. Williamson and Scott, "Further Observations," *Phil. Trans.*, 1894, vol. clxxxv., p. 863. Kidston, "*Sph. trichomatosum*," *Proc. Roy. Phys. Soc. of Edin.*, vol. ii., 1891. "*Sph. majus*, etc.," *Trans. Nat. Hist. Soc. Glasgow*, vol. vi., part i., 1899. Lignier, "*Equisetales* et *Sphénophyllales*. Leur origine Filicinéenne commune," *Bull. Soc. Linn. de Normandie*, vol. 7, Caen, 1903. Scott, "New type, etc. (*Sph. fertile*)," *Phil. Trans.*, B, vol. 198, 1905. "*Cheirostrobus*," *Phil. Trans.*, B, 189, 1897. Seward, *Fossil Plants*, vol. i., Cambridge, 1898. Here the literature up to date is fully given. Scott, *Studies in Fossil Botany*, 3rd edn., 1920, p. 75. Hirmer, *Handbuch d. Paläobotanik*, München, 1927, p. 348, where the literature is fully cited. Lady Isabel Browne, *New Phyt.*, Dec. 1933, "Noeggerathiae and Tingiae."

between the forks (Fig. 105, *A*). In some of them, and especially in the early forms, the leaves were divided into linear or even filamentous segments (*B*). Potonié points out that the earliest forms had narrowly linear, branched leaves, those of later occurrence had larger, more broadly wedge-shaped, and unbranched leaves: thus the area of the leaf increased in the rising geological scale, apparently by "webbing" of branches. On the other hand, a striking feature illustrated in the well-known *S. cuneifolium* was the heterophyllous character. Here on the same plant finely cut leaves may be found below, and broader wedge-shaped leaves above, while in the strobilus the leaves are again finely cut (Fig. 104). Commonly the members of one whorl were equally developed, but in the forms from the Glossopteris Flora, named *Trizygia*, they were unequal. Examples of the leafage of different types of Sphenophylls are shown in Fig. 105, *A*, *B*, *C*, *D*. The plants were fixed in the soil by diarch roots, which appear to have been borne on the nodes; but the details regarding them are imperfectly known. The whole plant seems to have been of a weak, straggling character.

The internal structure possessed greater distinctiveness than the external form, and showed a marked secondary thickening: this originated very early, so that the unaltered primary state is seen only in small twigs. Here a proto-stelic structure is seen, without any pith or conjunctive parenchyma. The primary xylem is of triangular form, the groups of protoxylem, either single or double, being at the projecting angles; or the angles may be duplicated, and a hexarch form be attained. The vascular system is strictly cauline: it passes through the nodes without any appreciable change of structure. A peculiarity of some importance for comparison with *Equisetum* is shown in the primary wood of the ancient species, *S. insigne*, from the calciferous sandstone: here a canal is formed at each of the three angles of the primary wood, presumably by disorganisation of the protoxylem as in

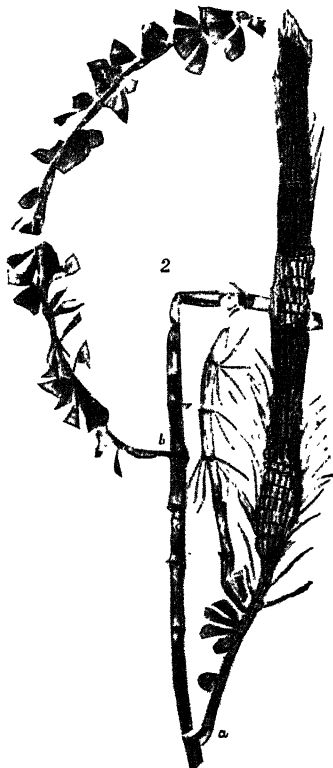


FIG. 104.

Sphenophyllum sp., branched stem, bearing linear and cuneate whorled leaves on different parts. The branch (a) terminates in a long and slender cone. Half natural size. (After Stur, from Scott's *Studies in Fossil Botany*.)

the Equisetales (Fig. 106). The cambial activity commences immediately outside the primary wood, and results in a broad zone of secondary wood, which completely surrounds the primary: it is traversed by continuous medullary rays in *S. insigne*, but in the later species these are represented only by little groups of thin-walled cells, which form, nevertheless, a continuous system. Outside the wood lie the phloem and the cortex, the latter

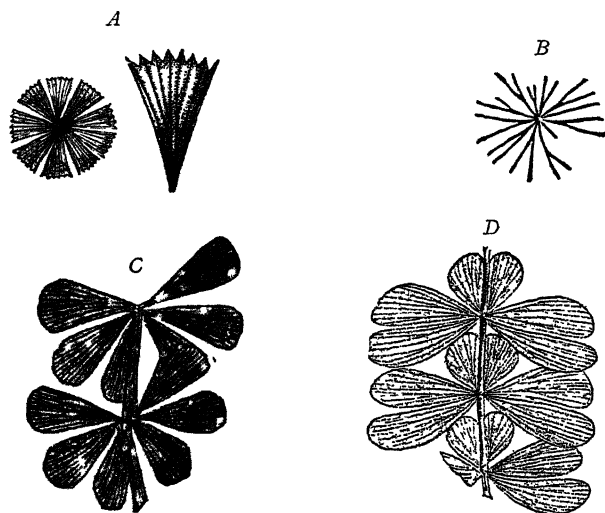


FIG. 105.

A = a leaf-whorl of *Sphenophyllum cuneifolium*, and one leaf of it somewhat enlarged. B = a leaf-whorl of *Sphenophyllum tenerrimum*. C = *Sphenophyllum verticillatum*. (From Potonié's *Lehrbuch der Pflanzenpaläontologie*.) D = "*Trizygia*" *speciosa*, Royle, from the *Glossopteris*-facies (after O. Feistmantel.)

showing a formation of periderm, which may be repeated, resulting in a scaly bark.

The leaves appear both from their size and from their structure to have been the assimilating organs, while the axis took little part in that function. Their parenchymatous tissue was, however, mechanically strengthened by bands of sclerenchyma. The vascular strands given off at the nodes branched within the cortex of the stem into strands which passed out as the veins of the leaf, though in some cases a single strand entered each leaf.

THE STROBILUS OF THE SPHENOPHYLLALES

The strobilus of *Sphenophyllum* was constructed on a plan similar to that of the vegetative shoot, with slight structural differences, and with the additional fact that spore-producing parts are present. These take the form of sporangiophores resembling in the main those of other microphyllous Pteridophytes. The most obvious external differences between the vegetative

shoot and the strobilus are that the internodes of the latter are shorter, and that the leaves, which are elongated as before, frequently show a distinct webbing below. The result is that the whole cone appears externally as a compact body, with the sporangiophores very adequately protected till

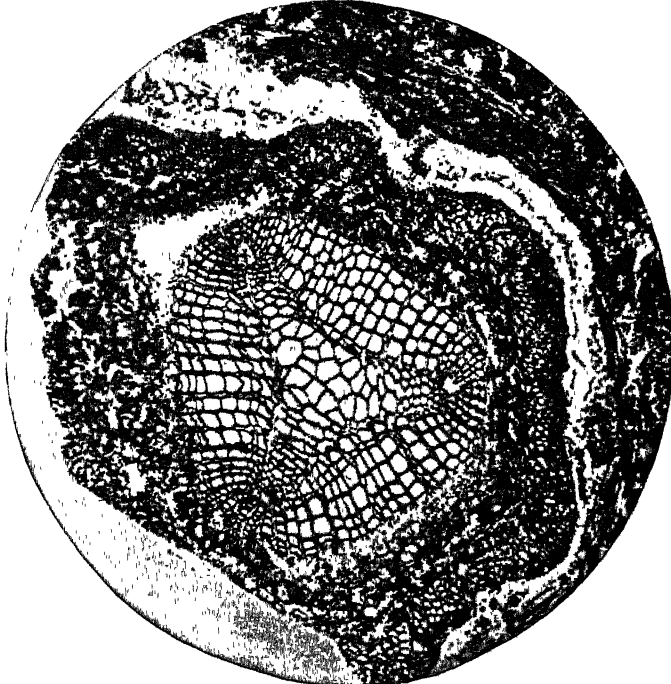


FIG. 106.

Sphenophyllum insigne. Transverse section of rather young stem, showing triangular primary wood with a canal at each angle, marking the protoxylem, then secondary wood, remains of phloem, and the primary cortex showing two of the furrows. \times about 30. From a photograph, *Phil. Trans. W. and S. Will. Coll.*, 919. (Block from Scott's *Studies in Fossil Botany*.)

maturity by the superposed whorls of bracts (Fig. 104). The sporangiophores are inserted opposite the individual bracts with such a degree of regularity that Hirmer sees in the two a collective unit, or "Sporophyll-einheit."¹ Moreover, they share a common vascular supply, which fact appears to support this view. But before its adoption it will be necessary to compare other Classes of Sporangiphoric Pteridophytes: and so test the point whether such a unit is so general a feature as to make this suggestion appear probable in this instance.

The various fossils described under the generic name of *Sphenophyllum* differ in the apparent number and in the insertion of the sporangiophores, as well as in the number of the sporangia borne on each of them. These

¹ *Handbuch der Paläobotanik*, p. 355.

differences offer curious analogies with those of floral construction in Angiosperms; but the latitude of variation here seen is such as would in Angiospermic flowers form the basis of much wider systematic distinctions than those of species or even genera. It is not improbable that upon this basis the genus will ultimately be broken up as detailed knowledge of it increases. Meanwhile the following are some of the types of disposition of the sporangia which have been described.

The simplest is that seen in *S. trichomatosum*, Stur, from the Middle Coal Measures, where the sporangia appear solitary near the axils of the subtending bracts, which were here of very narrow form. It is an open question whether the single sporangium was here really sessile, or was borne upon a vascular stalk, as in other species, but in this case exceptionally short. The evidence derived from impressions does not suffice to decide this point (Fig.

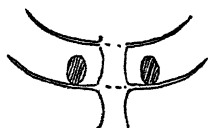


FIG. 107.
Sphenophyllum trichomatosum,
Stur. Diagrammatic figure of the
arrangement of the sporangia.
(After Kidston.)

107). From the guarded statements of Zeiller¹ it appears probable that a similar disposition of the sporangia is found also in *S. angustifolium* and *tenerrimum*, and it may be noted that these are all small species with narrow leaves. In the well-known *S. cuneifolium*, Stern (*S. Dawsoni*, Will. and Scott), each sporangium, single as in the foregoing species, is borne upon an elongated pedicel—the sporangiophore. The species presents several different types of cone, distinguished as forms α , β , γ according to their complexity. In form α the sporangiophores appear in section to be, as a rule, twice as many as the bracts of the subtending whorl; but in form β the number is larger (Fig. 108): each is traversed by a vascular strand which terminates at the base of the sporangium. The sporangiophores are inserted close to the base of the leaf-verticil, which is here webbed into a wide cup: and to this the pedicels may be adherent for varying distances upwards.

The vascular supply of the sporangiophores is derived by branching from that of the subtending bract. The foliar strand on entering the verticil divides to form a lower branch which supplies the bract and an upper which supplies the sporangiophores.²

A further complication is seen in *S. Römeri*, Solms Laubach, for in this cone two sporangia are borne on each sporangiophore, hanging down from its peltate distal end. The sporangiophores are disposed in three concentric verticils on each whorl of bracts, and are attached by short stalks each traversed by a vascular strand, which branches to supply the two sporangia (Fig. 109). The analogy with the sporangiophore of the Equisetales is more obvious here than in the previous cases, where only a single sporangium is

¹ *L'Appareil Fruct. d. Sphenophyllum*, pp. 31, 32.

² For details see Scott, *Studies*, p. 93. Hirmer, *l.c.* p. 355.

borne on each. It appears still more plainly in *S. majus*, Brongn., from the Middle Coal Measures, but as yet known only from impressions. This species is interesting from the fact that its strobilus is not a strictly definite

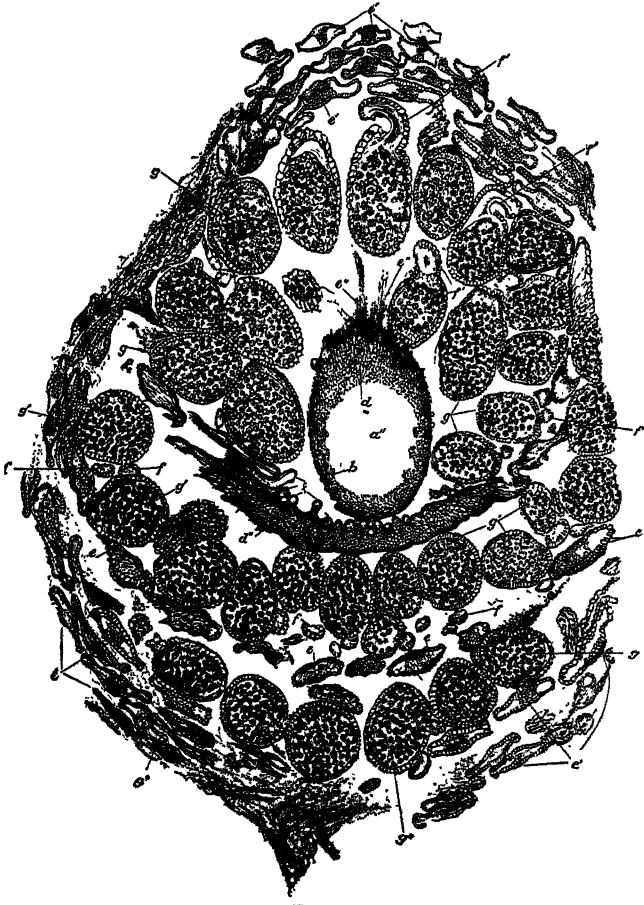


FIG. 108.

Sphenophyllum Dawsoni, form β . Obliquely transverse section of a cone, showing parts of three whorls of bracts. *a* = hollow axis (stele missing); *b*, *d* = cortex of axis; *e*, *e'* = bracts cut at different levels; *f* = sporangiophores, the innermost just springing from a whorl of bracts, which are here coherent; *f'* = sporangiophores in connection with their sporangia; *g*, *g'*, *g''* = sporangia of the three whorls. $\times 7$. After Williamson, *Phil. Trans. Will. Coll.*, 1049 B. (From Scott's *Studies in Fossil Botany*.)

one (Fig. 110). The number of the leaves in the whorl of the vegetative region is not constant: six to eight have been observed by Kidston. The branching of the leaves is variable, and even the two halves of one leaf may be unequal; the sporophylls are especially narrow as compared with the foliage leaves. The strobilus is characterised by the shorter length of the

internodes, though this is variable also in the vegetative region : a gradual transition occurs at the limits of the fertile tract, but without any sudden alteration of the size or form of the leaf ; the sporophylls stood out from the axis just like the ordinary foliage leaves, but were united at the base into a narrow sheath or collar surrounding the axis. The transition to the strobilus is plainly seen at the lower limit of the large specimen from the Brussels Museum, described and figured by Kidston ; towards the upper limit of the specimen, where the sporangia cease, the axis is continued in the vegetative manner, with longer internodes (Fig. 110). These facts plainly point to the absence of a highly differentiated strobilus, and the existence in this species

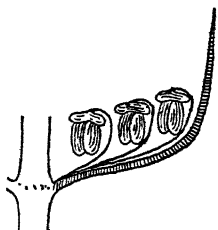


FIG. 109.
Sphenophyllum Roemerii. Diagrammatic sketch of the arrangement of the sporangia. (After Kidston.)

of a "*Selago*" condition, where the fertile region is a mere zone on a continued axis. Not only does *S. majus* stand as yet alone in the genus by the indefiniteness of its cone, but also in the character of its sporangiophores. One of these is borne near to the base of each forked sporophyll (Fig. 111) : the sporangia, which are 4-6 in number, but usually four, are grouped round a central attachment ; and though no elongated pedicel can be seen, still the fact that when they are removed from the bracts they still remain united in groups of four to six indicates that they had a common base. In favourable cases Kidston has been able to demonstrate that a radial line of dehiscence is clearly marked, corresponding in position to that of the synangium of *Psilotum*, to which the whole structure shows a remarkable resemblance.

As a further type, and not the least remarkable of this variable genus, may be mentioned the fructification of *S. fertile*, described by Scott (*Phil. Trans.*, B. vol. 198, 1905). It is characterised by the fact that both the "dorsal and ventral lobes are fertile" ; by which it is meant that the bract appears as bearing sporangia, as well as the sporangiophore which it subtends. Dr. Scott remarks that this is "more probably due to special modification than to retention of a primitive condition." "The sporophyll is also more complex than in other species, its lobes, both dorsal and ventral, dividing in a palmate manner into several branches, each of which constitutes a sporangiophore" (Fig. 112). An alternative reading of these facts will be offered after the Calamarian cones have been described (Chapters X and XXIX).

Lastly, there remains that remarkable cone from the Calciferous Sandstone of Burntisland, named by Scott *Cheirostrobilus*, and placed by him in relation to the Sphenophyllales, while recognising also its affinities with the Equisetales and Lycopodiales (*Phil. Trans.*, vol. 189 B., 1897). The vegetative system of the plant of which this is the fructification is still unknown. The cone itself is of large size, and shows greater complexity than any of the



FIG. 110.

Slab showing fertile shoots of *Sphenophyllum majus*, Bronn. sp. After a photograph from the specimen in the Musée roy. d'hist. nat. de Belgique, Brussels, and here inserted by permission of the director, M. E. Dupont. The curved specimen running up the middle of the slab shows a vegetative region with long internodes above and below, and a fertile region showing shorter internodes between them.

known sporangiophoric types. The robust axis has structural characters suggestive of a Lycopodinous rather than of a Sphenophylloid affinity: the central stele in transverse section has a solid star-shaped xylem-core, with twelve projecting protoxylem-groups, corresponding to the series of sporophylls. These were arranged in whorls of twelve, and were superposed; each consisted of three sterile lobes palmately divided, and it bore upon its upper surface, and inserted close to its base three sporangiophores; each of these was provided with four long pendent sporangia attached to its peltate distal end (Fig. 113). So far as the vascular connections are a guide, it may be concluded that the sporangiophores are appendages of the branched sporophyll, and especially of its middle segment, since a vascular strand supplying them originates from the bundle which runs into the middle segment of the sporophyll. This strand divides then into three,

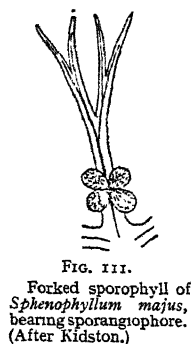


FIG. 111.
Forked sporophyll of
Sphenophyllum majus,
bearing sporangiophore.
(After Kidston.)

and one branch enters each of the sporangiophores (Fig. 114). Thus the course of the vascular bundles supplying the sporangiophores and bracts is essentially the same in *Sphenophyllum* and *Cheirostrobus*, though necessarily more complex in the latter.

There can be little doubt of the fundamental correspondence of the various types above described: they all coincide in the presence of spore-producing

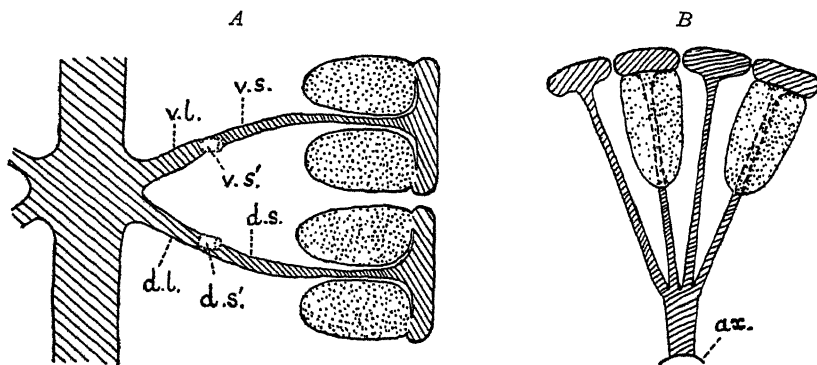


FIG. 112.
Sphenophyllum fertile. Diagram A, node in radial section, showing one sporophyll: v.l., ventral lobe; v.s., a ventral sporangiophore bearing two sporangia; v.s', stump of another sporangiophore; d.l., d.s., d.s', corresponding dorsal parts. B, one lobe of sporophyll, as seen in a transverse section of the cone, ax, axis. On two of the sporangiophores a sporangium is shown. (From Scott, *Studies*, Vol. I.)

parts subtended by sterile bracts arranged in superposed whorls; and notwithstanding their differences in number, and in the number of sporangia which they individually bear, it is safe to conclude that the sporangiophores are homologous throughout the series. Their similarity of general structure to the sporangiophores of the Equisetales is most clearly seen in *Sphenophyllum*

majus, or in greatly elongated form in *Cheirostrobos*. In point of position there is the difference of their being leaf-borne, as against the axial insertion of the Equisetales. The conclusion seems inevitable that the sporangiophore in these two phyla is a member of similar morphological rank, though in both phyla it shows variety in its exact position, and in its relation to the bracts.

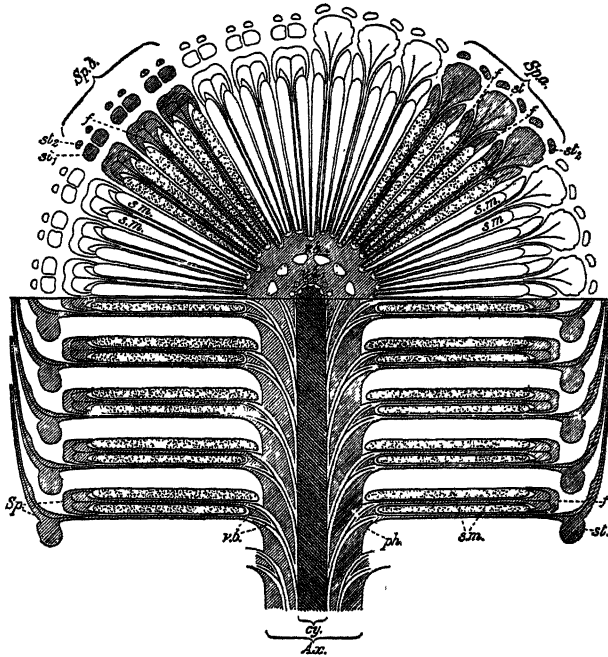


FIG. 113.

Cheirostrobos Pettycurensis. Diagram. The upper part in transverse, the lower in radial section; the position of the organs corresponds in the two sections. 1. Transverse section. Six complete sporophylls, each with three segments, are shown: *Sp.a*=section passing through sterile segments; *Sp.b*=ditto through fertile segments, or sporangiophores; *st*=lamina of sterile segment; *st1*=downward outgrowths of sterile laminae cut transversely; *st2*=their apices, transverse; *f*=peltate sporangiophores; *s.m*=sporangia. Note that in *Sp.a* each peltate lamina, *f*, is seen in two distinct lobes, with the sterile lamina between; *v.b1*, *v.b2*=vascular bundles of two whorls. 2. Radial section. The sporophylls are separated from one another for clearness' sake, in nature they are in close contact. *Ax*=axis of cone; *cy*=its stele; *ph*=base of sporophyll. Other lettering as in transverse section. The diagram is true to nature as regards proportions of parts, as well as their relative position. \times about 2. (From Scott's *Studies in Fossil Botany*.)

Here it will not be inapposite to point out in support of this view some features of structural similarity which exist between the Equisetales and the Sphenophyllales. They will be best illustrated in brief by the juxtaposition of Scott's two figures (compare Fig. 106 with Fig. 115). The former shows the transverse section of the ancient *S. insigne* from Burntisland, which differs from the later Sphenophylls in having a canal marking the position of the protoxylem at each angle of the primary wood; also in having continuous medullary rays in the secondary wood, and scalariform tracheides in place of

those with numerous bordered pits. Comparing this with Fig. 115, which is from the axis of *Calamostachys Binneyana*, there is a similarity in outline of the primary stele ; but as this is not constant in the species it cannot bear

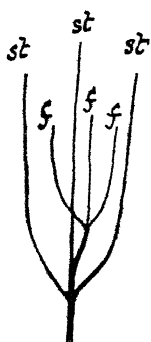


FIG. 114.

Diagram of the vascular supply to the sterile lobes (*st*), and to the sporangio-phores (*f*) in *Cheirostrobus*.

weight in the comparison. The points of importance are, the similar canals, of like position to those of *S. insigne*, and like them showing the position of the protoxylem ; the continuous medullary rays, and the similarity of the tracheides. These features appear to establish a real structural resemblance between the oldest of the Sphenophylls and the cone of a Calamite. But these comparisons are strengthened when the vegetative axis of *Protocalamites* is brought into the field (Fig. 138), for here centripetal xylem is seen in the vegetative stem.

Most of the Sphenophylls appear to have been homosporous. But there is evidence suggestive of heterospory in *Sphenophyllum Dawsoni* in which, in a given cone certain sporangia contain more numerous spores giving an average diameter of 83μ , while others contained fewer spores with an average diameter of 106μ : and it was noted that the former type occurs at the base of the strobilus, the latter distally (Thoday, *New Phyt.*, vol. v., p. 91). A more marked difference has been recorded in

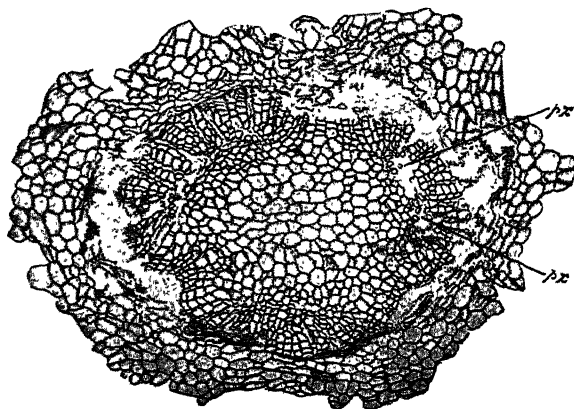


FIG. 115.

Calamostachys Binneyana. Transverse section of axis of cone, showing stele and part of cortex. Surrounding the pith there are six bundles, in groups of two, with secondary wood. *px* = protoxylem groups. \times about 60. *Phil. Trans. W. and S. Will. Coll.*, 1016. (From Scott's *Studies in Fossil Botany*.)

S. verticillatum by Zobel. In that species he found cones of two different types : the one with few large sporangia in each verticil (diam. 1.0 mm.) ; the other with many smaller sporangia (diam. 0.5 mm.). But since only one kind of spore has been as yet detected the evidence for heterospory is so

far unconvincing (Scott, *l.c.*, p. 96). The point has its interest for comparison with the heterospory well known as existing in *Calamostachys* (see p. 186, Fig. 145).

The gametophyte and embryology are unknown.

COMPARISON

A relation of the Psilotales to the Sphenophyllales was first suggested by Dr. Scott. Previously the Psilotales had been placed with the Lycopodiales. Such features as the dichotomous branching of the monostelic axis, the imperfect differentiation of the vegetative and fertile regions, and the relation of the sporangiophores of the Psilotales or of the sporangia of the Lycopodiales to the subtending sporophyll, were the chief foundations upon which this grouping rested. But the anatomical resemblance as well as the similarity of the spore-producing parts naturally drew the Psilotales and the Sphenophyllales together, and widened the breach between either of them and the Lycopodiales. So far were these last comparisons felt to be valid that, in the *Origin of a Land Flora*, the Psilotaceae and the Sphenophylleae were grouped as representing one phylum—the Sphenophyllales (*l.c.*, pp. 398, 434). But again the discovery of new facts, and even new types of vegetation, has affected the comparative value of the characters available for such a decision. The institution of the Class of the Psilophytales, with its clear relation to the Psilotales—the only Class of living plants with which such a relation is possible—has drawn the latter away from the nearer relation to the Sphenophyllales, and these two series will now be best studied as separate phyla, notwithstanding the many features of resemblance which they show.

The most striking difference is in the leaf-arrangement. In the Psilotales the appendages are alternate, and each is separately inserted on the axis; in the Sphenophyllales they are in superposed whorls, and webbed at the base. Too much weight must not be attached to such a distinction, particularly as we see within the genus *Lycopodium* certain species some with whorled others with irregularly alternate leaves; thus their arrangement may vary within a single genus of primitive Pteridophytes. The strictly whorled arrangement seen in the Sphenophylls is, however, shared by the Equisetales, a feature which draws these two classes together, and justifies Lignier's designation of them as the Articulatae (*l.c.*, p. 132). On the other hand, the Psilophytales and the Psilotales are both rootless, while the Sphenophylls and Equisetales are normally rooted in the soil. This difference sensibly widens the breach between the alternate-leaved and the whorled types.

Lignier, in a memoir of 1903 which from its originality has commanded wide attention, suggested, chiefly on the basis of the forked venation, that the

Sphenophyllales and Equisetales shared a common origin.¹ That the source of the Articulatae, under which title he included them both, may probably be sought among the most ancient of the Filicales. This was a very remarkable comparison, particularly in view of the fact that it ante-dated the discovery of the Psilophytales. At the time of its publication the very title of Lignier's memoir was a challenge. But if those "most ancient of the Filicales" represent the Psilophytales as at present known his thesis would now be less open to criticism than it appeared to be in 1903, particularly in respect of the sporangial characters. He laid, however, the weight of his comparison of the vegetative system upon the fact of the dichotomy in leaves, and on their venation. It cannot be assumed that all dichotomy sprang from a single phyletic source, and that a "Filicinean" source. Dichotomy is the simplest accommodation of form to increasing size. The whole series of facts adduced by Lignier, in this relation, appears to be consistent with the cladode leaves of Ferns and the microphylls of the Articulatae having shown independently this accommodation to increasing size; and they do not demonstrate their homogeny. The conclusion which will therefore follow will be, that foliar characters do not suffice to establish any near relation between the Articulatae and the Filicales.

It appears from the descriptions of the strobilus given above that the Sphenophyllales take morphologically a middle position between the Psilotales with their laxly constructed fertile shoots, and the Equisetales with their compact cones. The Psilotales again may be contrasted with the Psilophytales, in which the distal sporangia are as a rule isolated, and there is neither strobilus, nor sporangiophore, nor yet synangial grouping. The plants thus named cannot be held as constituting any simple or coherent evolutionary sequence; nevertheless they suggest a general progression that is of importance in the morphology of the Pteridophyta, viz., that from the isolated distal sporangium to sporangia grouped together, borne upon sporangiophores, and associated with bracts; in fact, from a diffuse fertile branch-system to a complex and closely packed strobilus. The essential feature in all such cases is the spore-producing organ itself: it is in respect of this that the Sphenophyllales display a variety of detail that is very suggestive.

In the description of them given above the different types have been taken in order of their complexity, ranging from the simple state of *S. trichomatosum* (Fig. 107) to the very complex state of *Cheirostrobos* (Fig. 113). In all of them, whether simple or complex, the median position of the spore-bearing organ relative to the subtending bract is constant, and the function is the same; therefore it may be held that, whatever the differences of complexity, the sporangiophore opposite any one single bract is homologous with any

¹ Lignier, "Equisétales et Sphénophyllales: leur origine filicinéenne commune," *Bull. Soc. Linn. de Normandie*, vol. 71, 1903.

other so placed. Consequently the Sphenophyllales give the opportunity for comparing the various degrees of branching which they show. These branchings, which are based on repeated dichotomy, have been specially studied by Hirmer, who, in addition to a detailed description of the known types, has attempted to visualise them by means of diagrams (*Handbuch der Paläobotanik*, pp. 348-376, Figs. 417-421). As a middle type in respect of complexity *Sphenophyllum Dawsoni* may be taken. The cone of this species appears in various forms which have been designated α , β , γ , and placed thus in order of the complexity of their sporangiophores. Hirmer refers the relatively simple structure of form α to a three-armed sporangiophore, resulting from successive serial and collateral forkings of the whole. Scott, however, states that no structure such as the three-armed sporangiophore has hitherto been observed in this cone (*New Phyt.*, 1929, p. 83). The difference of opinion probably arises from the fact that the forkings of the

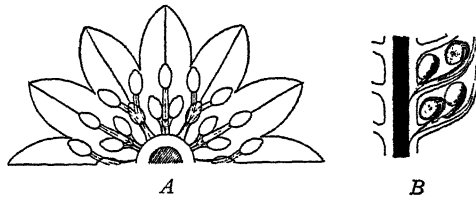


FIG. 116.

A. Diagrammatic view of half of a whorl of bracts and sporangiophores of *Sphenophyllostachys Dawsoni*, Will., form α , from the lower coal measures of England. B. Diagrammatic longitudinal section through part of the cone. Each bract subtends a branched sporangiophore. In the diagram the median branch of each is shown halved longitudinally; of the two lateral branches only that in the background is shown. (After Hirmer.)

trace, upon which the branching is based, are carried out in the cortex, before the trace emerges from the axis. Owing to mutual adjustment of the sporangiophores of each whorl it comes about that the two-armed branches lie alternately above and below the one-armed branch: by this means the best use is made of the available space (Fig. 116). In *S. Röemeri* the relations are as in form α , except that each branch bears two sporangia instead of one. The same principle, viz., repeated forking of the sporangiophores, underlies also the more complex branchings of forms β and γ . It extends also to *Cheirostrobus* (Figs. 113, 144), in which a still higher state of branching appears, and it affects also the sterile bracts. On the other hand, the rosette-like sporangiophore of *S. majus* may be held to be the result of a more condensed form of a similar branching (Fig. 111), while the single sessile sporangium of *S. trichomatosum* probably represents the product of a sporangiophore without any branching at all (Fig. 107). It will be noted that the simpler types of spore-producing parts occur on the smaller and simpler species, as might have been naturally expected. For directly or indirectly a nutritional basis will necessarily underlie these fluctuations of development of the spore-producing parts. On this ground a comparison may be drawn

between the facts of fluctuation seen in the Sphenophylls and those already described for the Psilotales (p. 125). In these it was seen how the development of the fertile twigs is variable, those seated at the limits of the lax strobilus being often simpler than those in the middle of the fertile zone. In both of these related Classes it may be concluded that the spore-producing parts are imperfectly standardised, and liable to fluctuate either in the individual, as has been seen in the Psilotales; or between species or genera, as in the Sphenophyllales. In either case there is evidence of a compact strobilus in the making. In this relation the state seen in *Sphenophyllum majus* is particularly suggestive: its relatively long sterile internodes contrast with the relatively short internodes of the fertile tract, and point to a telescoping change as leading to the compact type of strobilus. If that were so for the vegetative parts, may it not be anticipated that a parallel condensation of a lax fertile *Hostimella*-branch-system, such as is seen in *Asteroxylon*, may also account for the various types of branching seen in the sporangio-phores of the Sphenophyllales and of the Psilotales? The discussion of this question will be taken up in Chapter XXIX, after the other microphyllous Pteridophytes have been described. Meanwhile we see that the Sphenophyllales and the Psilotales occupy a middle position between the Psilophytales and the more definitely strobiloid types, in respect of the compactness of grouping of the appendages upon the axis.

CHAPTER X

EQUISETALES ¹

THE Equisetales are distinguished from the rest of the sporangiophoric types by the fact that their sporangiophores are inserted directly upon the axis, not on appendicular parts : in some cases they show a definite relation to the bracts which subtend them ; in others no such relation exists. Other less distinctive characters of the vegetative organs are : the constantly radial construction of the shoot, the elongation of the internodes which are longitudinally striated, the verticillate arrangement of the leaves, a high degree of branching, and a structure of the stele with a ring of isolated vascular strands : these collectively characterise the group as a definite one. As regards its past history, the evidences of the existence of the Equisetales extend back to the Devonian period, where they already showed a high degree of elaboration. But these plants formed a more conspicuous feature in the Carboniferous Flora, where they attained their maximum development in point of numbers as well as in size. Subsequently the type became less prevalent, till at the present day it is represented only by the cosmopolitan genus *Equisetum*, with its twenty to thirty species, showing remarkable uniformity of type. The essential characteristics of the living genus will be taken first, as it is susceptible of more complete study than the fossils ; these will be worked in later on a basis of comparison with what is seen in *Equisetum* itself.

¹ *Selected Literature on the Equisetales (General)* : A full citation of the earlier Literature is given in Von Goebel's *Grundzüge*, 1882, translated as *Outlines of Special Morphology*, Oxford, 1887. For the genus *Equisetum* see Rabenhorst's *Krypt. Flora*, "Luerssen," 1889, pp. 622-781. For Fossil Equisetales see Seward, *Fossil Plants*, vol. i., 1898, pp. 295-388. Campbell, *Mosses and Ferns*, 1918, chap. xii. Scott, *Studies*, 3rd edn., vol. i., 1920, pp. 13-72. Hirmer, *Handbuch d. Paläobotanik*, 1927, pp. 376-474. Von Goebel, *Organographie*, 1930, *passim*. (*Special Memoirs*) : Sadebeck, "Embryo," *Pringsh. Jahrb.*, ix., 1878, p. 1. Buchtien, "Proth. of *Equisetum*," *Biblioth. Bot.*, Cassel, 1887. C. E. Weiss, "Steinkohlen Calamarien," *Geol. Special Karte von Preussen*, 1876, 1884. Cormack, *Ann. of Bot.*, vii., 1893, p. 63. Jeffrey, *Mem. Bost. Nat. Hist. Soc.*, vol. 5, 1899. Gwynne-Vaughan, *Ann. of Bot.*, xv., 1901, p. 776. Eames, *Ann. of Bot.*, xxiii., 1909, p. 587. Barratt, *Ann. of Bot.*, xxxiv., 1920, p. 201. Kashyap, "E. debile," *Ann. of Bot.*, xxviii., 1914, p. 163. Campbell, "E. debile, Embryo," *Ann. of Bot.*, xlii., 1928, p. 717. Lady Isabel Browne, *New Phyt.*, vol. vii., 1908. "Interrelations of Pteridophyta," *Ann. of Bot.*, 1912, p. 663 ; xxix., 1915, p. 231, where literature on anatomy is fully cited : also *New Phyt.*, xix., 1920, p. 11 ; *Ann. of Bot.*, vol. xxxiv., p. 237 ; xxxix., 1925, p. 313. *New Theory of Calamarian Cone*, xli., 1927, p. 301, where the literature is fully cited.

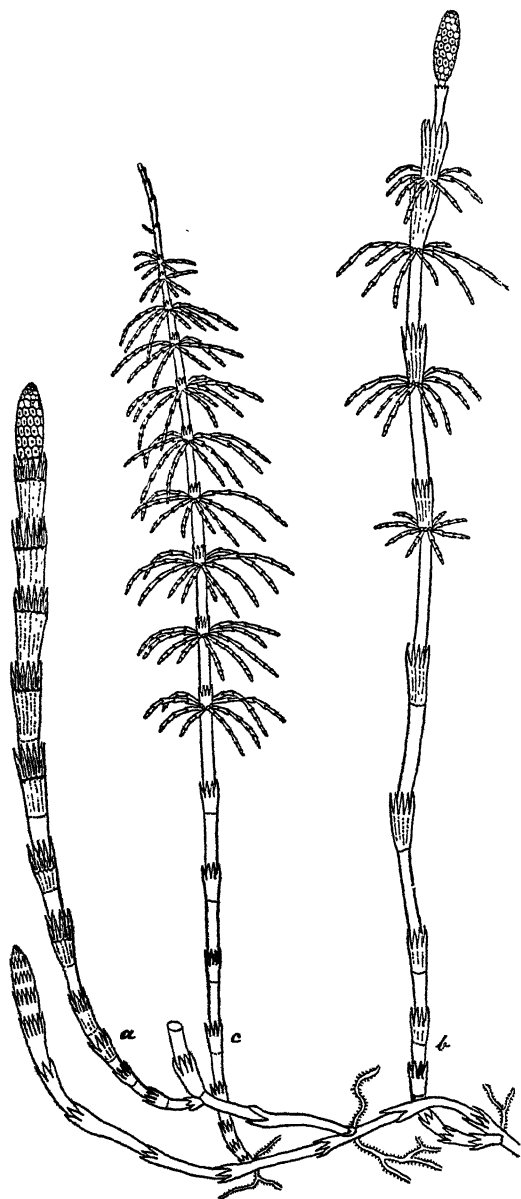


FIG. 117.

Equisetum pratense, Ehrh. Rhizome with unbranched fertile shoots (a), a fertile shoot which has begun to form branches (b), and a young sterile shoot (c). Natural size. (After Duval-Jouve, from Rabenhorst's *Krypt. Flora*.)

EXTERNAL CHARACTERS

It will not be necessary to describe the characters of the shoot in *Equisetum* in full detail, or the comparatively slight modifications of it upon which the species are distinguished: a brief account will suffice to indicate the essential features, for beneath them all lies a general unity of plan which is closely followed, whether the shoot be

underground or exposed to the air (Fig. 117). The axis is plainly the dominant feature of the shoot, and it is always of radial construction: it is terminated by a conical apex. Upon the vegetative axis the leaf-sheaths arise laterally, in acropetal succession, and distally they form a distinct bud. They are webbed, and when mature consist of clearly marked leaf-teeth projecting upwards from the cylindrical or conical sheath below (Fig. 117). As the developing internodes lengthen by intercalary growth of the bud thus constructed the leaf-sheaths separate, while the internodes themselves are then seen to be marked by flutings corresponding to the markings of the leaf-sheath next above: at the nodes the flutings of the successive internodes alternate. The leaves themselves are mostly dry and chaffy, while the tissues of the stem contain chlorophyll, and constitute the chief assimilating

tissue of the plant. The number of teeth in the sheath, their proportions, and their permanence or deciduous character may vary: the internodes may be swollen for storage purposes in underground stems, while on the aerial stems the extent of the chlorophyll-parenchyma, and the number and disposition of the stomata may fluctuate; but, putting aside such differences, which are only of secondary importance, the plan of the shoot is the same in all living Horsetails. It is a notable fact that in none of them is there

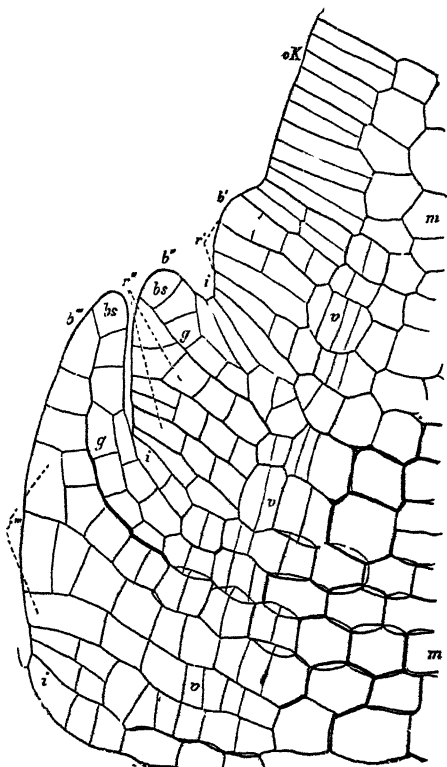


FIG. 118.

Equisetum maximum, Link. Left half of a radial longitudinal section below the apex of an underground bud (in September). *vK*, lower part of the apical cone; *b*, *b'*, *b'''* = leaves; *m* = pith; *v*, *v* = meristematic ring; *g*, *g* = cell-layer from which the bundles of the leaf-teeth arise; *i*, *i* = the first beginnings of branches. (After Sachs, from Engler and Prantl, *Nat. Pflanzenfam.*)



FIG. 119.

Equisetum sylvaticum, L., forma *polystachya*, Milde. Plant with 18 secondary strobili, in three whorls of branches which are normally sterile. Natural size. (After Luerssen.)

any departure from the radial symmetry of construction of the shoot, or from the verticillate disposition of the leaves.

The normal branching of the shoot is monopodial, and originates from cells lying immediately above the leaf sheaths, and in a position alternating with its teeth (cells marked *z*, *z*, in Fig. 118); the branches are therefore not truly axillary. The shoots thus initiated burst through the subtending sheath, giving the appearance of an endogenous origin, and on further development they repeat, though usually on a simplified scale, the characters of the original shoot. The branches thus formed are plainly accessory to the parent shoot.

The roots, excepting the primary root of the embryo, are formed in regular relation to these accessory buds, one root being initiated at the base of each bud: and thus the roots, though formed like the buds in definite positions relative to the other parts, are held none the less to be accessory also. Their further branching is monopodial. It is interesting, however, to note that in the ancient *Asterocalamites* dichotomy of the roots has been recorded (Hirmer, *l.c.*, p. 377): this may be compared with the dichotomy in the roots of *Lycopods*, and in *Ophioglossum*.

Both roots and shoots are susceptible of different degrees of development according to circumstances, with results which lead to striking external differences; and upon these the specific distinctions are partly based. Either shoots or roots may remain dormant though initiated: this is especially seen in the case of the roots in aerial parts, and of the lateral shoots in the parts that are underground. This circumstance provides specific characters: thus, in some species many or all of the branches may remain dormant, even on the aerial stems

(e.g., *E. limosum* and *hiemale*). It also contributes largely to the general aspect of the individual organism, as is clearly seen in the case of such species as *E. pratense* (Fig. 117). In other species again the development or non-development of the branches differentiates the vegetative axes from those which are fertile, as in *E. arvense* and *maximum*: in others the lateral branches on fertile axes are only delayed in their development, as in *E. palustre* and *sylvaticum*: in others again there is little difference as regards branching between the fertile and sterile shoots. But it has been shown experimentally by Goebel that even in so pronounced a case of the absence of lateral branches as the fertile axis of *E. arvense* the development of green lateral branches could be induced, by culture of the lower internodes in a moist chamber, when green assimilating branches were put out from the nodes, as in the vegetative shoot. The apparently branchless fertile shoot is thus brought into line with the ordinary branched type prevalent in the genus. Such facts indicate that in the first instance the branched condition was probably common for the genus.

The fertile strobilus of *Equisetum* is terminal on the axis, and is usually borne on the relative main axis only. Many cases exist, however, of the development of the strobili on lateral branches. This may be normal for certain species; but it also occurs occasionally in others, where a single terminal strobilus is normally present ("*forma polystachya*").¹ In the case of *Equisetum sylvaticum polystachyum* (Fig. 119), where numerous lateral branches usually sterile bear small strobili, Luerssen has been able to correlate the change with external conditions:² this is the next step to bringing its determination within the limits of experiment. On the other

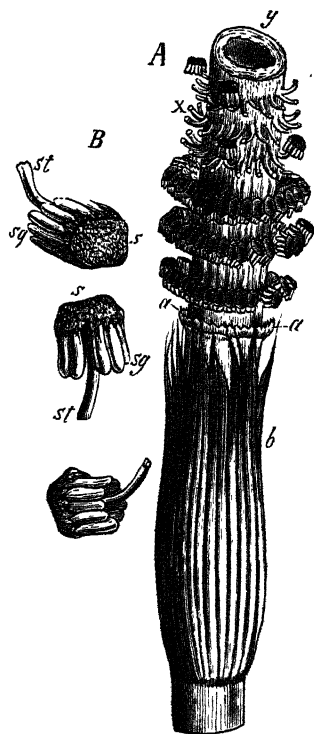


FIG. 120.

Equisetum maximum, Link. A, the upper part of a fertile axis, with the lower half of the strobilus. Natural size. b = the leaf-sheath. a = annulus. x = stalks of sporangiophores cut off. y = transverse section of axis. B = sporangiophores in various positions, slightly enlarged. st = stalk. sg = sporangia. s = enlarged distal end. (After Sachs.)

¹ For records of such developments in European species, see Rab. *Krypt Flora*, iii., p. 622, etc.; and especially Luerssen, "Beitr. z. Kenntn. d. Flora, W. and Ostpreussens," *Bibl. Bot.*, 1894, Heft 28.

² *L.c.*, p. 13.

hand, numerous cases have been recorded of the continued growth of the strobilus, at its apex, with a return to the ordinary vegetative characters.



FIG. 121.

Equisetum pratense, Ehrh. Shoots showing recurrent whorls of sporangiophores and of bracts. (After Milde.)

Such facts show that the lateral branches are not essentially different from the relative main axis, as regards the final end of spore-production ; also, that there is no absolute barrier between the vegetative and the fertile regions in *Equisetum*. Thus it requires no great effort of imagination to see in the shoot-system of *Equisetum* the result of repetition of a simple unit, the shoot, composed of axis and successive leaf-sheaths, and capable of spore-production by a terminal strobilus. The fundamental idea of the plant is thus carried back to the first shoot which originates with the embryogeny.

The strobilus itself consists of a continuation of the axis which bears it, and upon this the sporangiophores are disposed, but often with less regularity than rules in the case of the leaf-sheaths. The whole strobilus is normally occupied by the

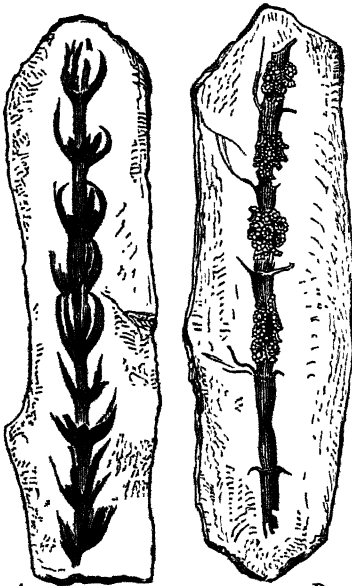


FIG. 122.

Phyllothea, Zigno. A, *Ph. equisetiformis* from Rovere di Velo, near Verona. B, inflorescence from Siberia, placed by Schmalhausen with *Phyllothea*. (After Solms.)

sporangiophores, without any intervening bracts (Fig. 120, *A*). The sporangiophore itself consists of a central stalk supporting a polygonal distal end: from the margin of this the sporangia hang in variable number round the stalk (Fig. 120, *B*). The spores are all of one type (Isosporous). At the base of the strobilus a ring-like structure is found—the annulus—which is like a reduced leaf-sheath, and it has usually been held to show a transitional stage between the vegetative leaf-sheaths and the first whorl of the sporangiophores, these being recognised as equivalent parts. Reasons will be advanced below for not accepting this apparently simple view.

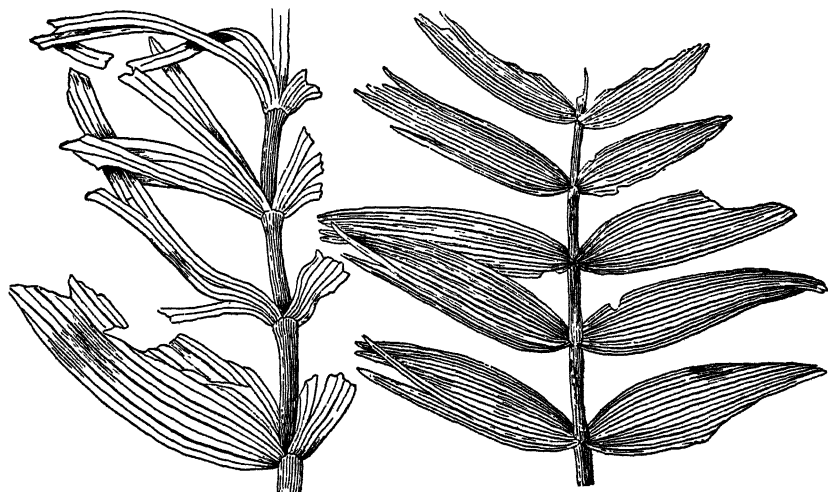


FIG. 123.

Schizoneura Godwanensis. Two-thirds the natural size. (After O. Feistmantel, from Engler and Prantl, *Nat. Pflanzenfam.*)

The strobilus of *Equisetum* is liable to variations of development, which have their importance in relation to certain fossil forms. The most notable of these is proliferation, the apex of the strobilus being continued as a vegetative shoot: the effect is thus gained of a fertile zone bearing sporangiophores, threaded upon an axis; or of a succession of such zones, separated by leaf-sheaths (Fig. 121). It is thus seen that the strobilus of *Equisetum* is not always that circumscribed terminal body which is typical for the living species.

The *Equisetum*-type has been recognised as far back as the Middle Coal Measures; but it is also represented by large forms, in the Mesozoic rocks. Related to it are two other fossil types: the genus *Phyllothea* of Permian age resembles *Equisetum* in the general features of the shoot, with its cup-like leaf-sheaths webbed at the base; but differing in the form of the leaves and in the fertile region. This is constructed on the general plan of *Equisetum*,

but with the strobilus interrupted at intervals by sheaths of sterile leaves, as in some abnormal conditions of *Equisetum* (Fig. 122). The other genus is *Schizoneura*, of Triassic age, characterised by the whorled leaves being associated in webbed sheaths, which may, however, be slit longitudinally to

the base. They thus form leaf-like lobes which stand off at a considerable angle from the axis (Fig. 123). The axis is marked by longitudinal grooves, which are continuous from internode to internode, thus showing that the leaves of successive whorls did not alternate. The fructification is unknown.

Most of the older Equisetal fossils, however, belong to the Calamarian type. These plants were often of dendroid habit, with secondary thickening of the stem, but with a similar primary construction of the shoot to that seen in *Equisetum*. A reconstruction of a leading type, by Hirmer, is shown in Fig. 124. It belongs to the group of the *Eu-Calamites*, and the drawing shows the horizontal rhizome, from which sprang a widely branched aerial shoot rising to some 30 to 40 feet in height. In this type the branches were continued to the base of the stem, the position of the lowest being marked by scars; they were arranged in opposite and alternating pairs. The rhizome and the base of the stem were furnished with numerous roots springing from the nodes, as in *Equisetum*. The branches of these Calamarians were

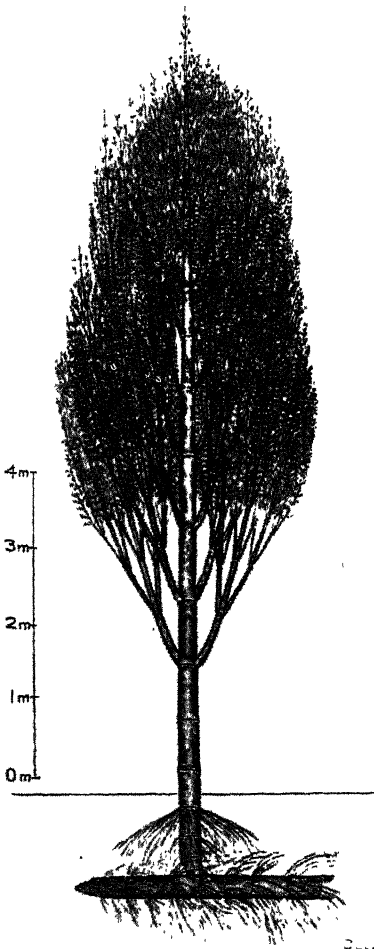


FIG. 124.
Reconstruction of plant of *Calamites* (*Eu-calamites*)
carinatus. Sternbg. (After Hirmer.)

highly ramified, and bore whorled leaves, while the strobili arose usually in complex inflorescences; but in the type named *Stilocalamites*, which shows a less freely branched habit, the strobili arose from the main axis itself.

The whorled leaves of the Calamarians were frequently webbed at the base, though often only slightly so, as in *Annularia*; but in *Asterophyllites*, which is traced back to the Devonian period, the leaves appear quite separate, and in widely divergent whorls. The leaves themselves were usually simple, as in *Equisetum*, though of greater dimensions, and accordingly more effective as assimilating organs; but among the earliest forms, such as *Asterocalamites* from the Culm, the leaves were branched in

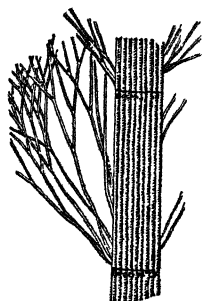


FIG. 125.

Asterocalamites scrobiculatus. Schlotheim (sp.) from the Culm. Fragment of a leafy shoot, reduced to half its natural size. (After Stur, from Zeiller, *Paléobotanique*.) Note that the fluting does not alternate at the nodes, showing that the leaves were superposed.

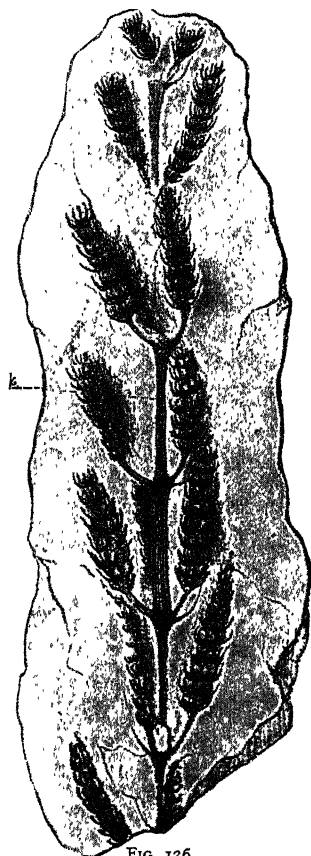


FIG. 126.

Palaeostachya pedunculata. Specimen from the coal-shales, showing a fertile shoot bearing about a dozen cones, and a few leaves. *k*=stem. About two-thirds natural size. (After Williamson, *Phil. Trans. Will. Coll.*, 1860.) From Scott's *Studies in Fossil Botany*.

repeated dichotomies (Fig. 125). Another feature, in which certain of the earliest forms differed from the later, was in the fact that the members of successive whorls were superposed, and did not alternate: for in-

stance, in *Asterocalamites* (Fig. 125). Such forms have been associated by Potonié as a family of "Protocalamariaceae." The facts would seem to indicate a primitive construction of the Equisetoid shoot as having relatively large and superposed leaves, effective as assimilating foliage: these were all separate from one another, and liable to bifurcation. The condition, as seen in the present *Equisetum*, might be understood to have been attained by reduction of the coalescent and simple leaves, which became also alternate instead of being superposed; meanwhile the assimilatory function was relegated almost entirely to the axis.

The Calamarian strobili were as a rule terminal on the axes, as in *Equisetum*, but they had a more elongated form (Fig. 126); sometimes they extended to a length of 30 cm. (Potonié). They differed also in their construction: the nearest to the *Equisetum*-type was that of *Archaeocalamites* (*Bornia*), characteristic of the oldest Carboniferous strata,

and of the upper Devonian (Fig. 127). Its strobilus was essentially like that of *Equisetum* in having no sterile bracts intervening between the whorls of

eight to ten sporangiophores. Scott remarks, however (*l.c.*, p. 62), that it is quite possible that bracts may have occurred in scattered whorls at long intervals, as was clearly the case in *Pothocites*, and in the Permian genus *Phyllothea* (Fig. 122). The whorls of sporangiophores in *Archaeocalamites* did not alternate, but neither did its whorls of branched leaves. In such types there appears to have been a more complete distinction between the vegetative and the propagative regions than is seen in other Calamarians.

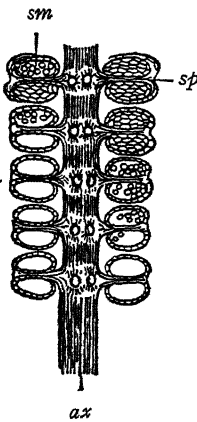


FIG. 127.

Archaeocalamites. Part of cone showing the axis (ax) in surface view, bearing superposed verticils of peltate sporangiophores (sp) without bracts. sm=sporangia. (After Renault.) From Scott.

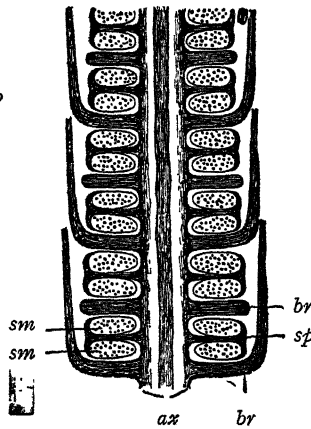


FIG. 128.

Calamostachys. Diagram of cone in radial section. ax=axis, which bears successive verticils of bracts (br), and peltate sporangiophores (sp). sm=sporangia borne on the sporangiophores. As the bracts are alternate with one another their upturned tips are only shown in every alternate verticil. (After Scott.)

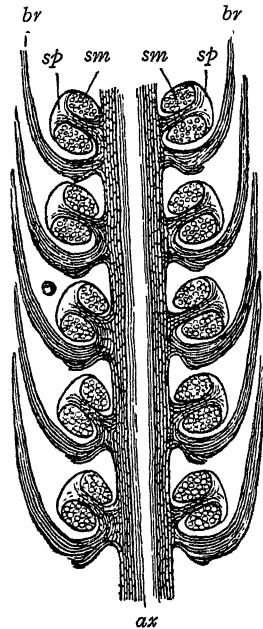


FIG. 129.

Palaeostachya. Diagram of cone in radial section. ax=axis, which bears verticils of bracts (br) with peltate sporangiophores (sp) in their axils. sm=sporangia. (After Renault.) From Scott.

The more prevalent type of strobilus among the early Equisetales was that in which whorls of bracts and of sporangiophores succeeded one another alternately. This is seen in *Calamostachys*, and it is well shown in *C. Binneyana*, which is a familiar type (Fig. 128). The sterile whorls are commonly composed of twelve coherent leaves, but thirteen have been counted: the sporangiophores are usually six, that is, half the usual number of the leaves of the sterile whorls; but seven and eight have been seen in single whorls of them, while no whorl of sixteen bracts has been seen. Hence it appears that the sporangiophores bear no strict numerical relation to the sterile bracts. The position of the bracts in successive whorls of them alternates; the successive whorls of sporangiophores, on the other hand, do not alternate,

but are placed one above the other in vertical rows. Hence it appears that there was no constant relation as regards radial position between the bracts of the Calamarian cone and the sporangiophores. Moreover, a tendency to multiply the number of the bracts in each whorl seems to have been a characteristic Calamarian feature. In *Calamostachys germanica* the narrow bracts were approximately three times the number of the sporangiophores in each whorl (C. E. Weiss). In the large cone described by Lady Isabel Browne as *Calamostachys magnae-crucis* there were usually about three bracts to every two sporangiophores, while in *C. Grand-Euryi* the bracts were as in *C. Binneyana*, about double the number of the sporangiophores. These examples will serve to illustrate the numerical instability of the appendages. The relation of the two parts as regards vertical position is also variable within the fossil Equisetales: for instance, in

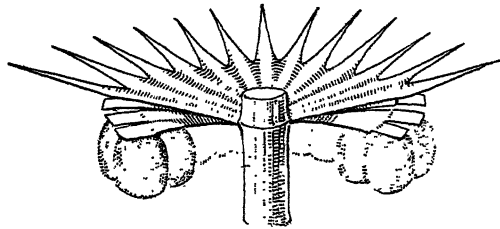


FIG. 130.

Cingularia typica, Weiss. From the Westphalian. Diagrammatic drawing of part of a shoot. \times about 2. (After Weiss.)

Palaeostachya the sporangiophores are inserted at the base of the internode (Fig. 129); in *Calamostachys* they are seated at the middle of the internode (Fig. 128), while in *Stachannularia* and *Cingularia* they are at the top of the internode, immediately below the next whorl of bracts (Fig. 130).

Such facts as these, here only briefly sketched, will have to be taken into account in discussing the morphology of the strobilus of the Equisetales, and in deciding the true character of the sporangiophores and bracts. But before this is entered upon the detailed structure, and as far as possible the development of these plants, must be examined.

ANATOMY

As the stem is the dominant feature of the shoot in the Equisetales the chief points of importance in their structure relate to it, rather than to the leaves or roots. Details will be described first for the living genus *Equisetum*, and these may then be used as a basis for comparison with those of the fossils. Together they may form a foundation for comparing the distinctive structure of this Class with that of other Pteridophytes.

The longitudinal fluting of the stem of *Equisetum* gives a sinuous outline to the transverse sections, and these will first be examined as from an internode, for there the structure is undisturbed by the insertion of leaves, branches, or roots. The characteristic uniformity in the general plan of the transverse section for three living species of *Equisetum* is shown in Fig. 131,

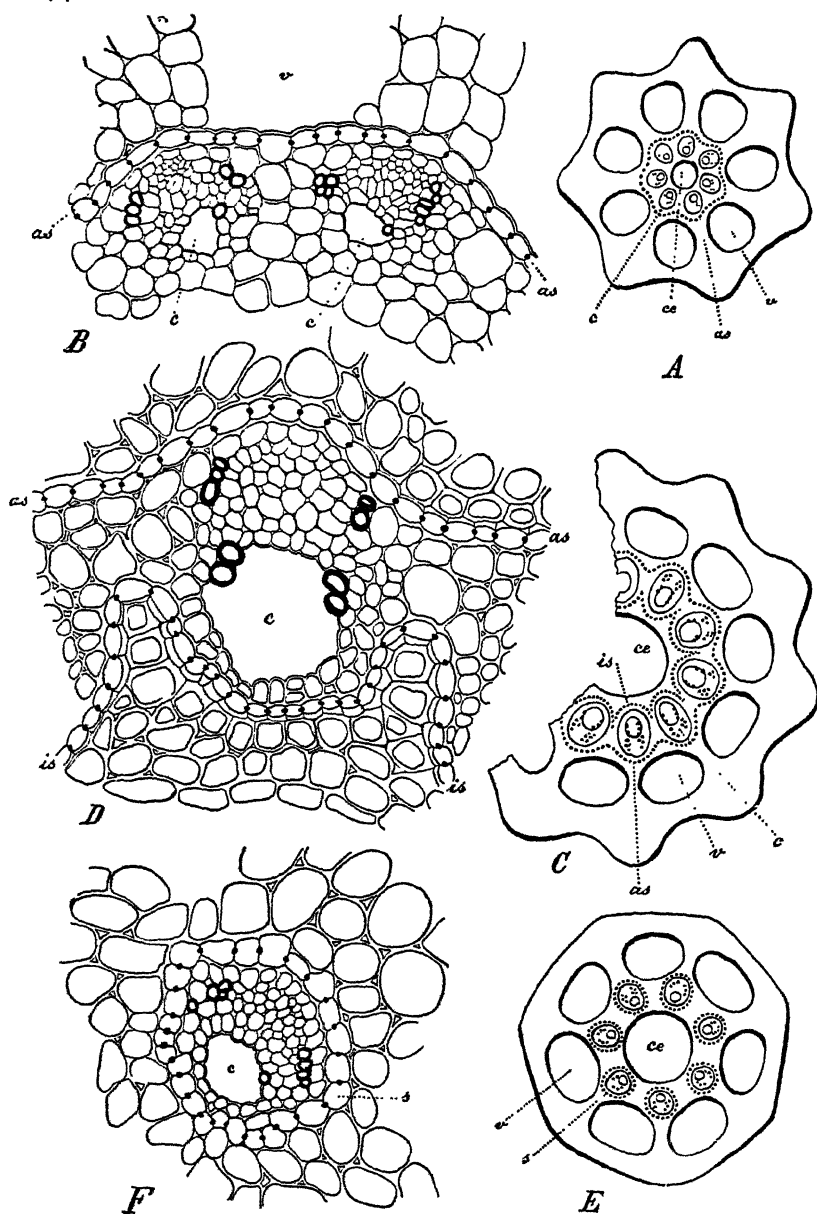


FIG. 131.

A, transverse section of the stem of *Equisetum palustre* ($\times 26$), and B, part of it $\times 160$. C, transverse section of the rhizome of *Equis. sylvaticum* ($\times 26$), and D, part of it $\times 160$. E, transverse section of the rhizome of *Equis. litorale* ($\times 26$), and F, part of it $\times 160$. ce=central cavity. v=vallecular canals. c=carnal canals. s=sheath of separate strands. as=outer, is=inner general endodermis: in A, C, and E the endodermis is indicated by a dotted line. (After Pfitzer.) From Rab, *Krypt. Flora*.

A, C, E. The main features are the sinuous outline ; the broad cortex, with its series of large air-spaces or vallicular canals (*v*), each opposite one of the concave channels of the outer surface ; and the central stelar tract containing a ring of vascular strands alternating with the *vallicular canals*, and each with its own central air-space which is consequently opposite one of the ridges of the outer surface : these are therefore named *carinal canals* (*c*).

Centrally is a large pith-cavity (*ce*). The endodermis is represented in these figures by dotted lines : it forms in *E. palustre* a general sheath surrounding the whole stele (*A*) : in *E. sylvaticum* the same, but with an inner endodermis delimiting the pith (*C*) : in *E. litorale*, however, there is a special endodermal sheath surrounding each separate strand (*E*). The external surface is covered by an ill-defined epidermis, which together with the thick-walled subjacent tissue forms a sclerotic band strengthening each projecting ridge. On the sloping sides of the ridges the strengthening tissue is interrupted by thin-walled chlorophyll-parenchyma, while here the epidermis bears peculiar stomata, each with two guard-cells and two subsidiary cells. Internally lie the vallicular canals of lysigenetic origin.

The large central pith-cavity, which is interrupted by diaphragms at the nodes, is surrounded by the ring of vascular strands, their number varying according to the species, or according to the rank and size of the stem in question.

The structure of the adult internodal strand is shown, with slight variants, in Fig. 131, *B, D, F*. All are constructed on the same plan : centrally lies the carinal canal with a few tracheides of protoxylem attached to its outer margin. Obliquely outwards from this lie right and left other groups of tracheides of metaxylemic type. These strands have been found to show

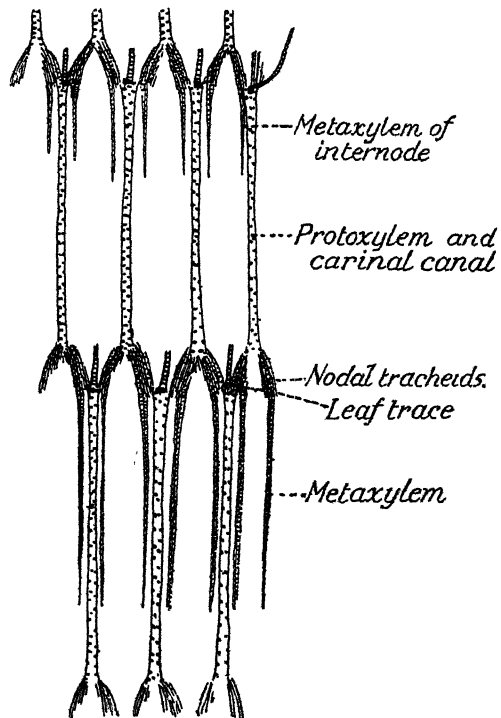


FIG. 132.

Scheme of Vascular System of *Equisetum*, after Miss Barratt, including the readjustments at two nodes. It suggests the relatively late development of the metaxylem, which gradually extends down the internodes ; their length is much reduced.

centrifugal succession of their tracheides, while their development starts from the upper node, and is continued downwards through the internode (Fig. 131). Between the two groups of metaxylem lies a tract of phloem. In all the Horsetails the strands are closely surrounded by endodermis, either a general sheath (*B*), a double sheath (*D*), or an individual sheath for each strand (*F*). The general scheme of the system of strands, with a suggestion as to the development as above described, is given in Fig. 132.

Before proceeding further it will be well to consider the structure of the apical cone from which the constituent tissues take their origin. The apex of

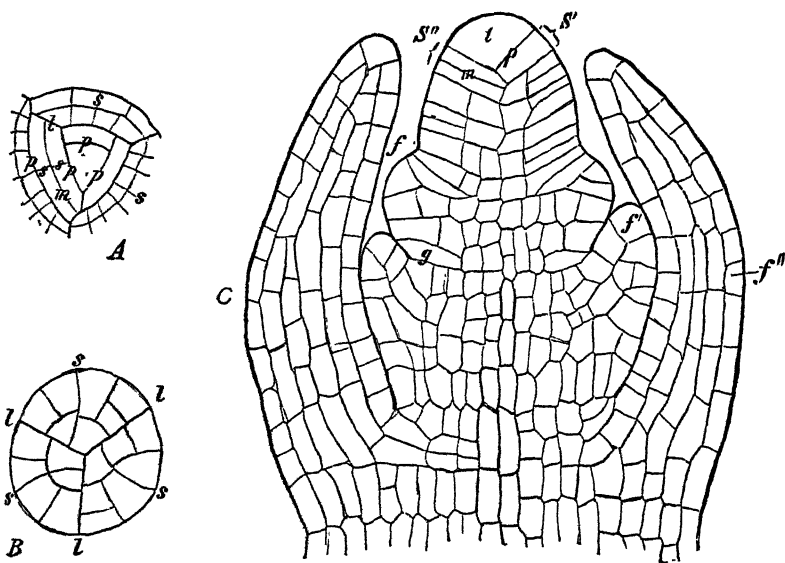


FIG. 133.

Sections illustrating the structure of the vegetative cone of *Equisetum arvense*, after Strasburger. *A* = as seen from above: the apical cell is triangular, and by successive cleavages parallel to its sides segments are formed. Each is further divided by walls parallel to the first. *B*, shows an optical section of the cone, immediately below the apical cell; *l* = lateral walls of the three segments; *s* = the anticlinal sextant-walls by which each divides into two. *C*, a median longitudinal section of the bud, showing the origin and relation of the successive whorls of leaf rudiments *f, f', f''*. *g*, a cell which gives rise to a lateral bud. *t* = apical cell; *p* = a principal segmental wall, defining a segment, *s'*; *m* = the anticlinal cleavage parallel to it which divides each segment. $\times 240$.

Equisetum is a classical example of segmentation with a single three-sided pyramidal initial cell (Fig. 133). In median section the apex projects beyond the youngest leaf-sheaths as a rounded cone, with its tip occupied by a single initial from which segments are cut off in regular succession. Viewed from above the cell is three-sided, and the segments which build up the axis below it are arranged in three rows, each corresponding to one of its sides (Fig. 133, *A*). The leaf-sheaths arise in acropetal succession by lateral outgrowth from the apical cone, each forming an annular cushion from which the leaf-teeth make their appearance as protuberances at distinct points. The

number of these varies in stems of different strength, and it bears no constant relation to the three rows of segments. Thus the segmentation does not dominate the number or position of the teeth; moreover, as the leaves of successive whorls alternate while the segmentation remains uniform, it seems impossible to trace any mutual relation between them and the apical segmentation: the two phenomena appear to be quite independent one of another. Each segment produced from the initial cell divides first by an anticlinal "sextant" wall (s), then each of the six products again divides by a periclinal wall. The result is six cells forming an irregular central column surrounded by twelve outer cells (Fig. 133, B). The former develop only pith; the cortex and vascular strands are derived from the outer series.

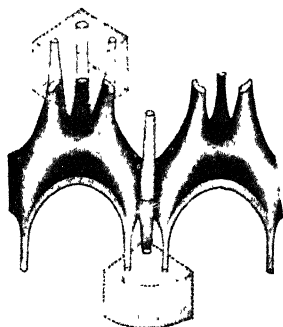


FIG. 134.

Diagram constructed by Mr. Gwynne-Vaughan to represent the conformation of the vascular tissue at a node of *Equisetum*. Above and below the node the groups of three strands, the median leaf-trace and the lateral metaxylem strands, are shown. In the centre the entry of a leaf-trace is shown, and its passage inwards to take its place nearest to the pith, while the metaxylem strands are lateral.

Hence the origin of the stelar tract, as compared with that of Lycopods, or protostelic Ferns, bears no constant relation to the apical cleavages. Such facts are important as showing that apical segmentation and development of parts or of tissues are not necessarily related to one another in vascular plants at large. (Compare Schoute, 1902: *Land Flora*, p. 178.)

In approaching the much debated question of the stelar structure seen in the adult shoot of *Equisetum* as a whole, of which we have thus far examined only the internodal strands in transverse section, it will be well to start from the sporeling (Barratt, *Ann. of Bot.*, xxxiv., 1920, p. 204). The stem in *E. arvense* is protostelic at the base, with a solid tracheidal core. This expands upwards to a solenoxyletic state, but the ring soon disintegrates to form distinct xylem strands corresponding in number to the next higher leaves. At first the strands are independent, but they become linked together at the nodes by oblique tracheidal tracts, which spring right and left from the base of the descending strands, as each whorl of alternate leaf-traces reaches its node of insertion. This gives rise to the cylindrical system characteristic of *Equisetum*, the nodal complications of which have presented difficult problems. Transverse sections of the adult internodal strands have been seen to present slight

variants, but all are constructed on the same general plan (Fig. 131 *B, D, F*): and this is suggested by Gwynne-Vaughan's diagram in its relation to the node (Fig. 134).

The first nodal problem is that of secondary thickening, which is so prominent a feature in the dendroid Calamarians. At the node of *Equisetum* a considerable mass of tracheidal tissue is found closely related to the nodal readjustments already described: it is shown in Gwynne-Vaughan's diagram,

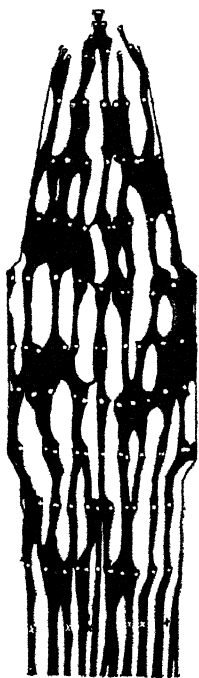


FIG. 135.

Longitudinal reconstruction of the xylem of a cone of *Equisetum giganteum*; axial xylem black, traces and parenchyma white. \times about 7. (After Lady Isabel Browne.)

Fig. 134. The arrangement of the tracheides in radial rows, as seen in transverse section, suggested that they were of cambial origin (Cormack, *Ann. of Bot.*, vii., 1893, p. 65). But more exact observation has shown that the tracheides are really primary, and their apparent increase as well as their arrangement are due to displacement of primary cells in course of development (Barratt, *l.c.*, p. 217). A more difficult question is as to the nature of the internodal bundle: whether or not it is a structural unit. Gwynne-Vaughan suggested that it is a composite structure. He found that of the three strands of xylem the carinal strand alone passes out at the node as a leaf-trace; and he describes how the two lateral strands are really cauline, passing right and left at each node, to continue as lateral strands in the next higher internode. He further suggested that the lateral strands may be taken as representing remnants of a primitive central mass of centripetal wood. This would involve two structural points: (i) a centripetal development of the metaxylem strands, and (ii) a crossing of those strands on the outer surface of the nodal xylem (compare Gwynne-Vaughan's diagram, *Land Flora*, Fig. 212, p. 388). A re-examination of these points of fact has shown that his suggestion is not upheld. Eames in 1909 contended that the internodal strand is a structural unit, representing the much reduced internodal primary bundle of the Calamites (*Ann. of Bot.*, 1909, p. 587). His position has been adopted on the basis of further observations by Lady Isabel Browne (*New Phyt.*, xix., 1920, p. 11), and by

Miss Barratt (*Ann. of Bot.*, xxxiv., 1920, p. 213). The probability is that most primitive Equisetaceous forms possessed well-developed centripetal wood, as Gwynne-Vaughan himself suggested, and that what is seen is a mere relic in which the centripetal feature has been lost. This will accord with the fact that groups of medullary tracheides seem to be not uncommon in the cones of *E. maximum* (Lady I. Browne, *Ann. of Bot.*, xxix., 1915, p. 231, etc.). The whole story leads back to the solenoxyllic ring and finally to the primitive protostele, of which an indication remains only in the youngest stages of the sporeling. So far as the centripetal development is concerned the state here seen in *Equisetum* is comparable with that of the vascular strands in a Dicotyledon.

How then are we to regard the gaps which intervene between the internodal bundles? They have been taken by Jeffrey to be ramular gaps; but Miss Barratt states that the actual areas of the xylem in which replacement of tracheides by parenchyma has taken place have no necessary relation to the insertion of leaves or branches (*l.c.*, p. 232). Certainly this is so in the strobilus of *Equisetum*, where neither leaves nor branches exist, other than the sporangio-phores, and yet xylic gaps are present (Fig. 135). The best comparison is probably with those xylic "perforations" well known in the solenosteles of advanced Leptosporangiate Ferns. Our conclusion from study of the living *Equisetum* will therefore be that its vascular system represents only a very attenuated remnant of a scheme based ultimately upon a protostelic origin.

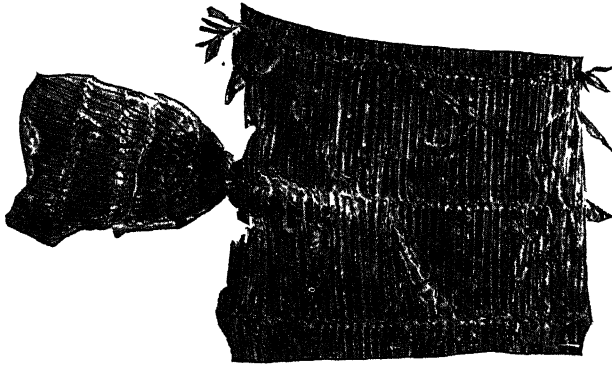


FIG. 136.

Calamites suchowii. Medullary cast, showing three nodes, on one of which the cast of a branch is borne. Below each node, and between the furrows, the prints of the infranodal canals are seen. About $\frac{2}{3}$ of natural size. (After Stur, from Scott.)

So attenuated a vascular structure as that seen in the relatively small living Horsetails would not suffice for the mechanical or the physiological support of large dendroid plants, such as the *Calamites* (Fig. 124). In them cambial activity has met the difficulty of increasing size. For *Calamites* itself the case has been succinctly stated by Scott: he remarks that the Calamite, so far as anatomy goes, is simply an *Equisetum* with secondary thickening. The cambial increase commences at the nodes, and extends thence through the internodes. The result may be a woody mass of great bulk, composed of tracheides with their pits limited to the radial walls, and with a general arrangement much like that of the Coniferae of the present day (Scott, *l.c.*, p. 26). It is divided up into bundles, with the principal rays between them of large size. It is this feature which gives rise to the markings on those most familiar objects of the coal period, the Calamitean casts (Fig. 136). Such casts represent the details of the surface limiting the pith-cavity, not the external surface of the stem. Their most conspicuous features are the longitudinal ridges which mark the position of the principal rays, while the furrows correspond in position to the vascular bundles themselves. It is seen

in Fig. 136 that these marks alternate at the nodes, as the vascular strands do in *Equisetum*. The relation of the secondary zone to the primary bundles, and of these to the pith is made clear by the photograph of an actual section of a young twig of *Calamites* shown in Fig. 137; here the primary bundles are, as in *Equisetum*, opposite to the zone of secondary tissue, in which the bundles are separated by broad rays. For further details reference should be made to Scott's *Studies*, or to other works on Fossil Botany.

In his *Pflanzen-palaeontologie* (p. 205) Potonié established a comparison between the secondary vascular tissues of the Calamariaceae and the Sphenophyllaceae by mentally doing away with the central mass of primary xylem

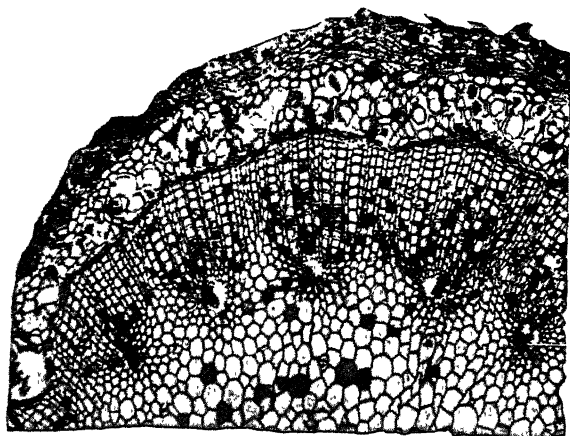


FIG. 137.

Calamites sp. Part of a transverse section of a young stem, showing pith, cortex, and five vascular bundles, each with a canal at its inner edge. In some of the canals remains of the spiral tracheides can be seen. Beyond the secondary wood, and next the cortex, are traces of the phloem. \times about 40. (After Scott, from a photograph by Farmer.)

that exists in the latter. Gwynne-Vaughan suggested that by inverting this procedure, and considering it possible that the ancestors of *Equisetum* may have possessed a xylem that extended to the centre of the stem, one is led to derive their structure, as it exists at present, from the modification of a stele with a solid central mass of centripetal xylem such as that of *Sphenophyllum* or of certain *Lepidodendreae*. This suggestion raised the question whether any Calamarian stem is known in which the hypothetical primary xylem is better represented, and is shown to be centripetal in its development? In 1901 Scott described a new species, *Protocalamites pettucurensis*, which gave the requisite answer. It comes from the Calciferous sandstone of Burnt-island.¹ The interest depends on the fact that each vascular bundle possesses a distinct arc of centripetal wood on the side next the pith of this very ancient

¹ *Brit. Ass. Report*, 1901, p. 849.

fossil (Fig. 138). The carinal canals are present as in an ordinary Calamite, and contain, as usual, the remains of the disorganised protoxylem. They do not, however, as in other Equisetales, form the inner limit of the wood; but xylem of a considerable thickness, and consisting of typical tracheides, extends into the pith on the inner side of the canal, which is thus completely enclosed by the wood. Hence, starting from the spiral tracheides of the protoxylem, there was here a considerable development of the xylem in a centripetal as well as a centrifugal direction. This was the first case of centripetal wood observed in a Calamarian stem; it serves to furnish a structural link between the Palaeozoic Equisetales and the Sphenophyllales.

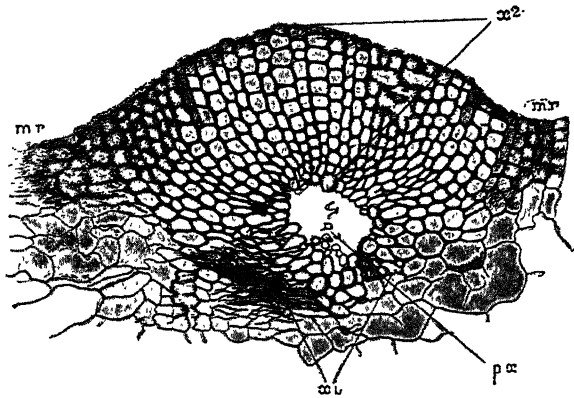


FIG. 138.

Protocalamites pettucurensis. Transverse section of the xylem of a vascular bundle in the stem. *px*, protoxylem; *x²*, secondary wood; *x¹*, centripetal wood, on the inner side of the canal; *mr*, medullary rays. \times about 60. (After Scott.)

The facts and arguments contained in the preceding pages clearly indicate the line of comparison of the stelar state of the Equisetales with that of the other Pteridophytes. The axis is monostelic, as in other primitive forms. It presents the appearance of a mere attenuated remnant of the probable archaic state of the protostele. Comparison makes it probable that in place of the solid xylem-core, which is seen in other phyla to be the primitive condition, the central part has become parenchymatous: in the early fossil, *Protocalamites pettucurensis*, the change had advanced so far as to reduce the volume of the xylem, though a centripetal remnant still persisted, and serves to indicate the probability of a protostelic origin, comparable to that condition seen in some Lycopodiales and in the Sphenophyllales. In the ordinary Calamites, as well as in *Equisetum*, the change has advanced so far that no remnants of the centripetal wood are to be recognised, and the presumption that they ever existed would itself be uncertain were it not for the confirmation brought by the fossil from the Calcareous sandstone. But together the evidence appears conclusive, and the result is to place the Equisetales, which have so long been a structural problem, in line with other strobiloid forms:

they, like the rest, have probably sprung from a protostelic ancestry. Physiologically the changes involved appear as a natural result of life in a semi-aquatic and muddy habitat, while the reduction of the leaves from effective assimilatory organs as they appear to have been in the early *Calamites*, to the protective sheaths of *Equisetum*, would also harmonise with the anatomical change contemplated.

The chief structural interest in *Equisetum* lies in such features of the axis as have been described. As regards the leaves, it may suffice to say that their structure points to a probability of reduction from a condition more effective for photosynthesis than that which they now show; and this was their state in some at least of the *Calamites*, where a well-developed palisade parenchyma is found, with numerous stomata on the flat adaxial surface (Scott, *l.c.*, Fig. 15, p. 36). The roots of *Equisetum* are essentially of the Fern-type, though with some peculiarities of their own. It may here be remarked that the roots of the *Calamites* show in their primary structure striking similarity to those of *Equisetum*, including the double endodermis; but they possess in addition a cambial thickening, and this is quite in keeping with the secondary growth of the axis which they supported.

THE STROBILUS

As with the vegetative organs, so also with the strobilus it will be well to take first the details for *Equisetum*, and then to relate them with those of the

Calamarians: for naturally the development can best be followed in the living plants. In *Equisetum* the axis, which is about to produce a strobilus, ceases active growth in length, retaining a conical form: the sporangiophores arise upon it in acropetal order, as convex swellings (Fig. 139). The details show some variation in different species: they are here described for *Equisetum arvense* and *limosum*. In the first stages the sporangiophores appear in the longitudinal section of a cone not unlike the sterile leaf-sheaths, involving, as seen in longitudinal section, some six cells, which grow out with a fan-like tracery and repeated anticlinal walls (Fig. 140, *A*). This similarity has been used as an argument favouring the view that the sporangiophore and

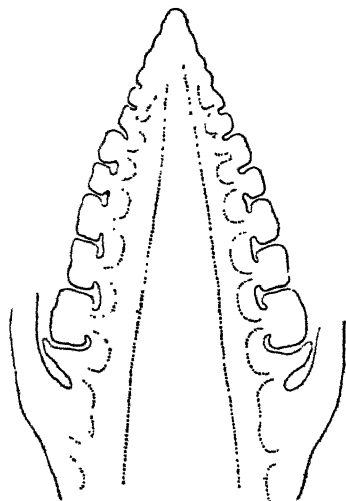


FIG. 139.

Half-developed strobilus of *Equisetum arvense*, in longitudinal section, taken at end of October. $\times 50$. (After Hofmeister.) The annulus is shown immediately above the last leaf-sheath.

the bract-leaf are results of "metamorphosis" of essentially the same part, a point which will be taken up later. Single superficial cells near the margins of the convex outgrowths are early recognisable as the parent cells which give rise to all the essential parts of the sporangia, though adjoining cells also grow out together with these to form the sporangial body: the origin of the sporangium is thus of the eusporangiate type (Fig. 140, *A, B*). At an early stage there is active growth in the middle region of the sporangiophore, which results in an inversion of the young sporangia, so that they come to point with their apices towards the axis. Each central cell of a sporangial outgrowth

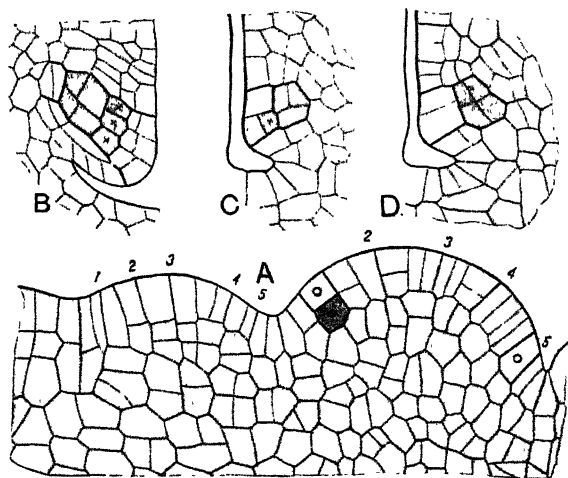


FIG. 140.
Equisetum arvense, L. *A*, radial longitudinal section of part of young strobilus, showing two sporangiophores in a very young state. *B, C, D*, individual sporangia, in older stages, cut in median section. $\times 200$.

first divides periclinally (Fig. 140, *A*): the inner cell gives rise only to a portion of the sporogenous tissue, the outer undergoes further division, first by anticlinal, later by periclinal walls (Fig. 140, *B, C, D*). The inner products thus formed share with the product of the inner cell already described in constituting the large sporogenous tissue, which, though entirely derived from the single parent cell, is not defined by its first periclinal wall: it is indicated by shading in the figures, while the products of the subsequent periclinal divisions are marked with a cross. Transverse sections at the stage represented in Fig. 141, *A*, show the sporogenous tissue in a central position surrounded by several rather irregular layers forming the sporangial wall (*B*). The size and construction of the sporangia, even of those in near juxtaposition, may vary greatly. As the sporogenous group enlarges a layer of cells immediately adjoining it externally becomes glandular in appearance, and develops as the tapetum (Fig. 142, *A*). Later the cells of the sporogenous

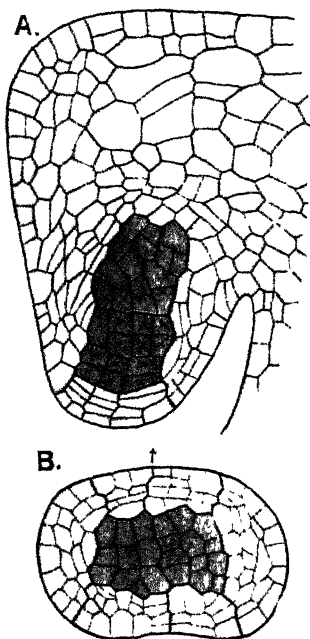


FIG. 141.

Equisetum arvense, L. A, section traversing a sporangium in median longitudinal plane: the cells marked (x), like those in Fig. B, are traced in origin from segmentation of superficial cells subsequent to the first periclinal division. B, a similar sporangium cut transversely. $\times 200$.

traversed from the stalk upwards by a vascular strand, which branches in the

tissue itself separate, and round themselves off as spore-mother-cells; but it is only about two-thirds of these cells which undergo the tetrad-division, about one-third of them shrivel and become disorganised, their substance mingling with that of the tapetum, which becomes intrusive as a multinucleate plasma into the interstices between the spore-mother-cells (Fig. 142, B): the fertile cells which remain are nourished by this as they develop into the mature spores. Finally, the superficial cells of the wall become indurated and spirally thickened, while those within it, excepting at the base of the sporangium, are disorganised. The mature sporangium, consisting thus of a single layer of cells of the wall, and containing the ripe spores which are all alike, dehisces along a longitudinal line facing inwards towards the stalk, which line had previously been defined by the cell-structure.

Each of the sporangiophores, from which the sporangia thus depend, is

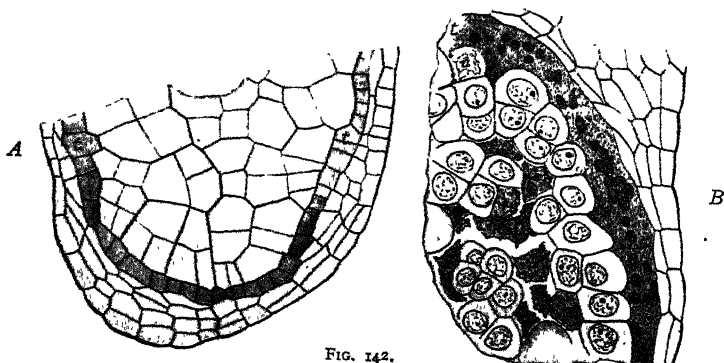


FIG. 142.

A, apex of sporangium of *Equisetum limosum*, L., showing the sporogenous cells, surrounded by the tapetum (t), and sporangial wall. B, shows part of an older sporangium with its tapetum (t) still clearly defined, though the individuality of the cells is lost: within this the sporogenous tissue, of which certain cells (a) are abortive. $\times 200$.

enlarged head, and each branch terminates immediately below the base of one sporangium. The sporangiophores are in close juxtaposition while young,

and thus the sporangia are effectively protected. At the base of the strobilus lies the annulus, which completes the investment of the lowermost series of sporangiophores: it has as a rule no vascular supply (Fig. 143). Goebel has pointed out this protective biological use of the annulus; also that at the apex the highest sporangiophores may be imperfectly developed and con-crescent, forming a terminal cap: the protection of the young sporangia is thus very complete.

The number of sporangiophores in the *Equisetum*-strobilus is not strictly defined, nor is their arrangement on the axis according to any constant rule: though in small strobili, such as that of *E. scirpoides*, and in the basal regions of larger species there may be regularity of arrangement in whorls, and of alternation. This is, however, lost in the upper regions of the cone (Fig. 120). The number of

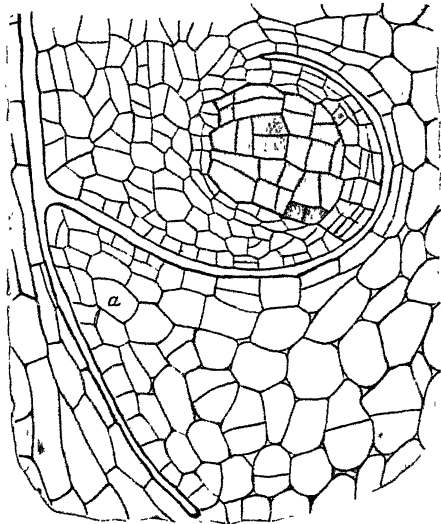


FIG. 143.

Equisetum limosum, L. Median longitudinal section of a sporangium at the base of the strobilus, together with the annulus (a). $\times 200$.

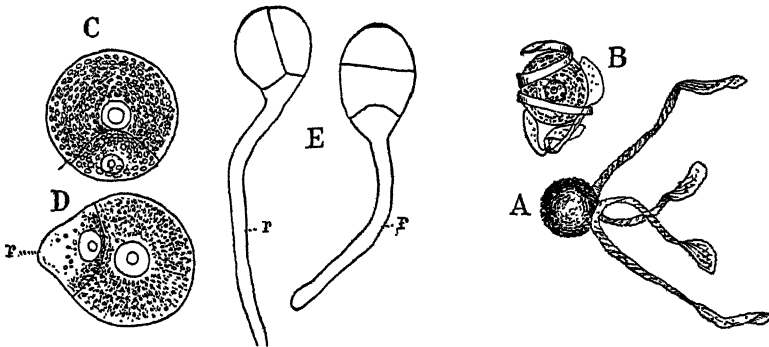


FIG. 144.

A, ripe spore of *Equisetum maximum* Lam., with expanded elaters. $\times 180$. B, similar spore placed in water. $\times 180$. C, D, germinating spores, $\times 360$. E, older stages of germination, $\times 180$; r, primary rhizoid. (After Campbell.)

sporangia on each sporangiophore is also variable: it is usually larger in *Equisetum* than in the Calamarians. The further development of the spores follows the usual course of tetrad-division; but each at maturity is of globular form, with no trace of ventral ridges. The spores of *Equisetum*

are peculiar in the development of their external wall: an innermost coat of cellulose is enclosed by an exospore, and externally four hygroscopic elaters, formed from the perinium, are attached in pairs to a central point. The expansion of these elaters on ripening aids the dehiscence of the sporangium by means of a ventral slit, while their hygroscopic movements secure the shedding of the spores in groups, rather than singly (Fig. 144).

In the Calamarians the position and structure of the mature sporangiophore, and of the four sporangia which they very constantly bear, are so

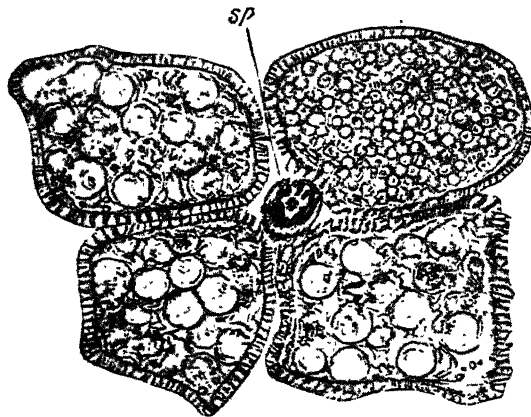


FIG. 145.

Calamostachys Casheana. Tangential section, showing four sporangia grouped around their sporangiophore (*sp*). Three contain megaspores and one microspores. $\times 30$. *Phil. Trans. W. and S. Will. Coll.*, 1587. (From Scott, *Studies in Fossil Botany*.)

similar to those of *Equisetum* that there can be no doubt of their true homology. The relation of the sporangia to the stalk of the sporangiophore (*sp*) in *Calamostachys Casheana* is shown in Fig. 145. All species of *Equisetum* are homosporous; there is, however, in some species of the Calamites evidence of heterospory in point of size of the spores; further, in *C. Binneyana* Scott has noted the abortion of certain spores of a tetrad: this taken with the difference in size of the spores in the closely related sporangia shown in Fig. 145 indicates the way in which heterospory may have originated in a palaeozoic genus. In this respect *Calamostachys* was in advance of *Equisetum*.

GAMETOPHYTE AND EMBRYO

The spores of *Equisetum* may germinate directly they are shed, or even before it (Fig. 144). They produce autotrophic, dorsiventral prothalli, which are characterised by the formation of numerous lobes. The prothalli are generally dioecious, but sometimes they may be monoecious, or perhaps rather andro-dioecious. The male prothalli are usually small and the lobes few (Fig. 146, II.). The antheridia arise in succession, and are more or less

sunk in the tissue. The sperms are large, spirally coiled, and multiciliate, with a well-marked blepharoplast (III.). The female prothalli are larger (I.), with numerous lobes at the base of which the archegonia arise: they are protected by a second lobe formed later opposite to the first. The archegonia originate on the lower surface of the thallus, as in Ferns; but by subsequent growth they are forced to the upper side. They are of the same type as those of the Ferns, with a sunk venter and projecting neck; but there is no

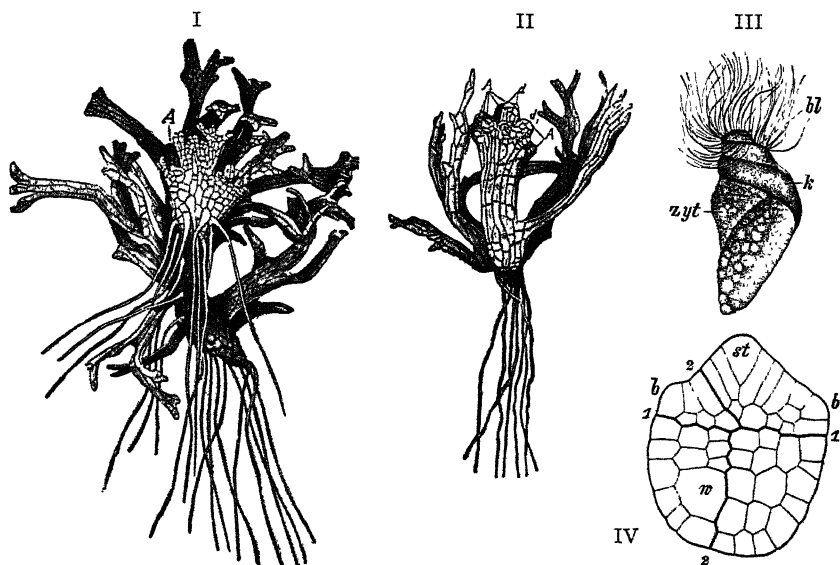


FIG. 146.

Equisetum pratense. I., Female prothallus from the under surface, showing the archegonia (A). II., Male prothallus with antheridia (A): *d*, cover cells of antheridia, after Von Goebel. I., $\times 17$, II., $\times 12$. III., *Equisetum arvense*, spermatozoid; *k*, nucleus; *bl*, cilia-forming blepharoplast with cilia; *zyt*, cytoplasm; \times circ. 1250, after Sharp. IV., *E. arvense*, embryo: *1*, *1*, basal wall. The stem and first leaf-whorl arise from the upper half, and the root (*w*) from the lower. $\times 165$. (After Sadebeck.)

basal cell formed by the first segmentation, and there is only a single neck-canal-cell. The four distal cells of the neck elongate greatly, separating at maturity with a hooked form (Fig. 147, VI).

The embryology of *Equisetum* bears a special significance, because this genus is the only representative of the articulate Pteridophyta in which it has been, or is ever likely to be, followed in detail—the rest being known only as fossils. The axis of the fertilised archegonium is approximately vertical, though there may be variants from this. The embryology is exoscopic, a feature which is shared with the Bryophytes. Some variety in the details of the embryology has emerged as the field of observation has been extended over different species. The classical description is that of Sadebeck, in 1877-8, for *E. arvense* and *palustre*, and it may be used as a basis for comparison (Fig. 147). In these species the basal wall (*b*, *b*), which first

cleaves the zygote, appears approximately horizontal, marking thus early the polarity of the embryo, and dividing it into epibasal and hypobasal halves : the shoot arises from the former, the foot from the latter. The absence of a suspensor simplifies the embryogeny as compared with that of certain other Pteridophytes. The attention should be fixed primarily upon the origin of the apex of the stem, since this is the dominating feature of the embryo. According to Sadebeck's description the epibasal half of the embryo divides into octants by walls at right angles to one another : one of those octants takes the lead over the others, and it is this one which gives rise to the axis with its tetrahedral apical cell, after the manner of the adult shoot. The product of this octant soon forms the greater part of the epibasal region (Fig. 147, IV.). Those octant walls which define it take their natural place as the earliest steps in the segmentation of an apical cell seated as nearly as possible centrally within the epibasal hemisphere. The polarity of the embryo thus asserts itself from the first cleavages in these species of *Equisetum*. The first leaves arise from a ring-like sheath, as three (or sometimes two or four) teeth. That sheath is described as originating partly from the remaining three octants of the epibasal half, but partly also from the lower portion of that which gives rise to the axis : in point of fact it encircles the apical cone (Fig. 147, III.). But it seems quite unnecessary to attempt to allocate the several teeth, or even the sheath itself, to definite octants, particularly as the number of the teeth is variable. It is more natural to regard the whole epibasal hemisphere as formative of the shoot : from this the stem-tip originates at an approximately central point, by the simplest possible steps of segmentation, which happen to involve octant-cleavages ; and the peripheral region of the epibasal hemisphere as a rule gives rise to the first leaf-sheath with its teeth. The shoot thus established continues its growth directly upwards, forming successive leaf-sheaths, followed by accessory branches. The hypobasal half of the embryo meanwhile becomes slightly distended as the "foot," which remains in contact with the prothallus after the first shoot and root have emerged. The first root in *E. palustre* and *arvense* originates laterally in the hypobasal hemisphere (Fig. 147, w).

The description given above relates to the species observed by Sadebeck ; but differences of detail have been described for other species : for instance, Jeffrey noted that in *E. hiemale* the first root originates from the epibasal hemisphere. The greatest divergences from the regular segmentation recorded by Sadebeck have, however, been found by Campbell in *E. debile*, though even here some examples were seen in which there was an almost perfect octant-formation. He found that the embryo often took a flattened form, and its first or basal wall may vary in position from horizontal to vertical. The shoot-apex and probably the root also are of epibasal origin, the whole of the hypobasal portion forming the very large foot. In general the organs of the young sporophyte of *E. debile* are differentiated later than

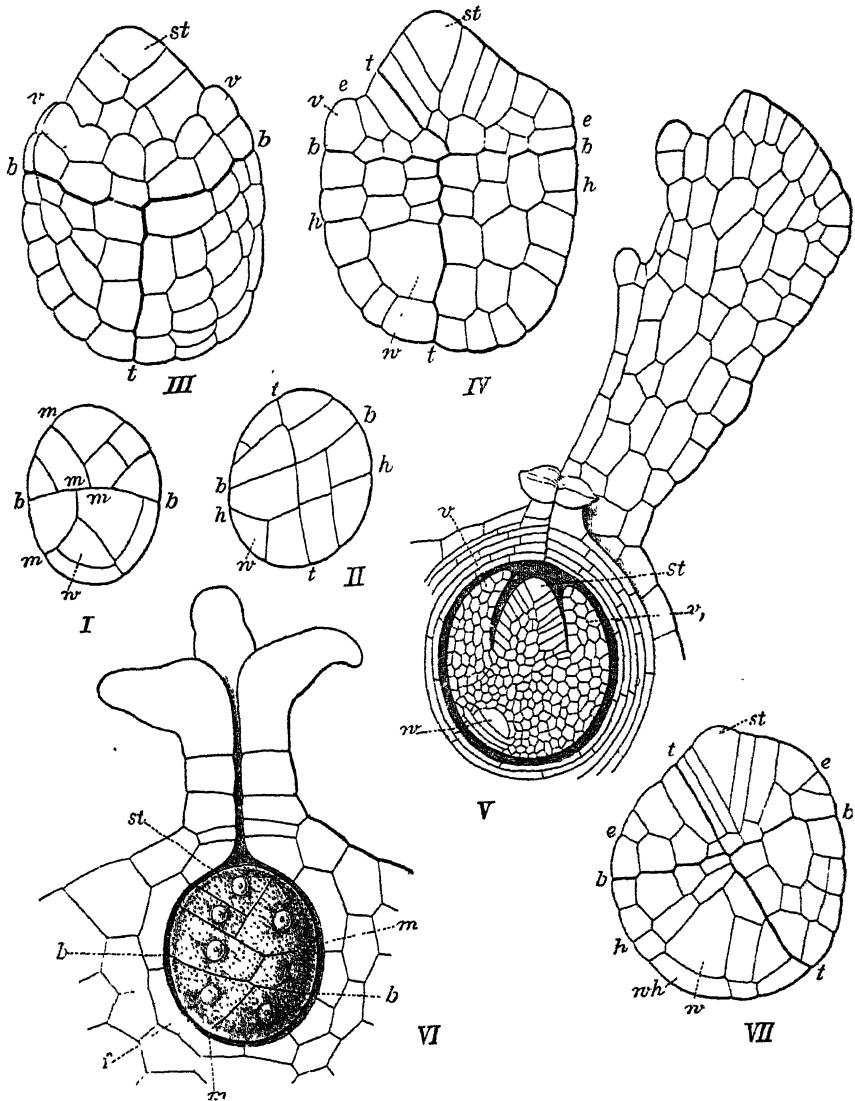


FIG. 147.

Embryo of *Equisetum*. I-IV., *Equisetum arvense*, L. I. and II., the same embryo in different positions: in I, the median wall is visible, in II, the transverse wall. $\times 300$. III.-IV., a more advanced embryo showing development of the stem and leaf-sheath. $\times 250$. V., an embryo still further developed, but not dissected free from the prothallus, and showing the orientation relatively to the archegonium. *st*=the stem apex; *v*=the first leaf-sheath; *w*=the root. $\times 98$. VI. and VII., *Equisetum palustre*, L. VI.= young embryo still in the archegonium, stem and foot are visible. $\times 300$. VII.=an embryo further advanced, and dissected free, and orientated 90° as compared with VI. The root (*w*) and stem (*st*) are visible. $\times 300$. *b*=basal wall; *t*=transverse wall; *m*=median wall; *e*=epibasal and *h*=hypobasal region; *v*=the first leaf-sheath. (After Sadebeck, in Engler and Prantl, *Nat. Pflanzenfam.*)

in *E. arvense*. All this points to a less clear relation of those organs to the primary cleavages, and the drawings of Campbell suggest some higher degree of independence between the initial cell-cleavages of the embryo and the morphological determination of its parts than Sadebeck had recognised. He, in accordance with the custom of his time, based his interpretation upon a regular relation of these parts to the early cleavages : and as a consequence he drove a direct comparison between the results of his own observations on *E. arvense* and *palustre* and the embryology of the Leptosporangiate Ferns, which was already well known. He concluded from the facts at his disposal that all Vascular Cryptogams share a uniform plan in the development of their embryos, and he has been followed in this by many later writers. But since Sadebeck's time the distinction between megaphyllous and microphyllous types has emerged. Whatever view may be taken of the origin of these distinct types, it should not be assumed that their embryology will accord consistently with any set segmental scheme. A more elastic comparison than that instituted by Sadebeck, and continued by others, will have to be followed, particularly in the case of microphyllous types. It will be best in them, and particularly in *Equisetum*, to take the facts as they stand, without ulterior interpretation in terms of the embryos of Ferns.

In point of fact the embryo of *Equisetum* appears as a more or less spindle-like body, one end of which grows onwards as the stem-apex, the other is attached to the prothallus. Upon this spindle appear an acropetal series of ring-like leaf-sheaths bearing distal teeth, which do not correspond to the primary cleavages of the embryo or its growing apex, either in position or in number. Meanwhile at some indeterminate level, sometimes hypobasal, sometimes epibasal, a root appears laterally. If we wish to compare this embryo of *Equisetum* with some other archegoniate type we should do well to leave the megaphyllous Ferns alone, and to turn to the rootless and leafless embryo of *Tmesipteris*, which like *Equisetum* is exoscopic. We have seen how, though ultimately the plant is microphyllous, the embryo itself is leafless, appearing as a naked spindle, divided into hypobasal and epibasal regions by a transverse basal wall (Fig. 100). The root is a feature which *Tmesipteris* does not possess. We may see in the embryo of *Tmesipteris* the naked essential of the embryo of *Equisetum*, which is the simple spindle. This comparison directs attention to the building up of a more complex organism than *Tmesipteris* from simple beginnings : for it may readily be conceived how the successive foliar sheaths of *Equisetum* may have been superposed upon a pre-existent spindle, such as we see to-day in the juvenile stage of *Tmesipteris*, and that roots have been added laterally (see Chapter XXVI).

The primary shoot of the embryo of *Equisetum* is limited, and ceases to grow after forming 6 to 12 internodes with their leaf-sheaths (*E. hiemale*) ; but meanwhile a shoot has been formed which emerges below the first whorl

of leaves, giving the appearance as though it were endogenous. The second shoot similarly gives rise to a third, the succession increasing in size till at last an adult shoot is attained. This branching of the sporeling appears to be general for the genus, and it may be compared with what is seen in the Psilophytales (Figs. 78, 79). A question arises as to the origin of these accessory shoots. Examining the point in *E. debile*, Campbell states that the bud arises endogenously from the root, and he gives illustrations which accord with that view. Von Goebel remarks that this mode of origin is improbable, and requires further detailed proof. An alternative suggestion would be that, as in the normal branching of the adult shoot, the endogenous origin is only apparent; and that the origin of this first bud is also really axillary to the lowest leaf-sheath, which is actually continued down deeper than the observer had believed. If this were so then the embryology of *Equisetum*, interpreted as above, would appear as one of the most natural and direct of all Pteridophytes; being exoscopic, and the initial polarity passing direct, without curvature, to the erect primary shoot. By the successive juvenile branchings of the same type as the first, the final end of sporogenesis is delayed; but the gradual accession of strength which they show leads at last to a strong shoot which is terminated by a fertile cone. These events may be held as marking the transition from adolescence to full maturity.

MORPHOLOGY OF THE CONE OF THE EQUISETALES

The morphology of the cone in the Equisetales remains to be discussed. The chief problem relating to it will be as to the nature of the appendages: for the axis upon which they are borne is continued directly up from the vegetative stem, and presents essentially the same structure, though with certain differences of detail. The most important of these is the absence of elongated internodes in the cone, so that the appendages are closely grouped together. The form of the appendages in *Equisetum* has been shown in Fig. 120, and those for certain selected fossils of the Class in Figs. 127-130. From these illustrations it appears that two distinct types of appendage may be present on the fertile stems, viz., leaf-like bracts and sporangiophores. In the Calamarian cones as a rule both types are associated together; but in *Equisetum* and *Archaeocalamites* only sporangiophores are found in the fertile tract, without the associated bracts. The question will be what is the real nature of these two distinct types of appendage, which thus vary in their distribution? Are they diverse forms of a single fundamental type of organ, or are they themselves historically and essentially distinct?

A view of the strobilus of *Equisetum* which has been widely held is that it is a product of metamorphosis of the sterile shoot, and that the sporangiophore is derived from a sterile leaf modified to perform the office of spore-production, while the annulus, as an intermediate structure, marks the

transition from the sterile to the fertile appendages. That the two types of appendage are homologous has lately been re-stated by Von Goebel (1930, *l.c.*, p. 1255). But before the homology of the leaf-teeth with the sporangiophores is accepted the grounds upon which it is based must be examined. They are : (i) the similarity of cell-structure on first origin ; (ii) the similarity of position relatively to the axis ; and (iii) the existence of transitional states from the one type to the other. A comparison of Fig. 118, which shows the origin of leaf-sheaths, with Fig. 140 showing the origin of sporangiophores, may be held to demonstrate the essential similarity of place and method of initial outgrowth of both ; though there is some difference in bulk, the sporangiophore being the larger. There is, however, divergence of development at once, after the initiation is passed. In the foliage leaves only the acroscopic side of the primordium is involved in the formation of the leaf, while the basiscopic side takes its share in the cortication of the internode. But in the formation of the sporangiophore the whole of the primordium takes part, and the growth is so distributed as to mould the peltate form : there is no expanded leaf-surface. The early divergence of the two is doubtless related to the difference of definitive form and function, and it suggests that if they be homologous, in any of the various degrees, the distinction will have been founded very early in the evolutionary history. Experimental evidence bearing on the third head has been brought by Von Goebel. He has shown by suitable culture that a young fertile cone of *Equisetum* may be transformed into a vegetative shoot ; moreover, at the transition intermediate forms between the two types of appendage may be produced (*l.c.*, p. 1240, Fig. 1314). Even in nature such states are not infrequently seen : isolated sporangia and even imperfect sporangiophores may be borne on the annulus, which was itself regarded by him as a last leaf-sheath imperfectly developed at the transitional region from the vegetative to the fertile shoot. A natural inference from this would be that the transitional abnormalities prove that the two parts are really homologous.

The strength of the view stated in reference to *Equisetum* by Von Goebel lies in the fact that it is supported by all the three lines of evidence above noted. If it were not for the fossils, which are not accorded such place in his discussion as many think that they deserve, his conclusion might never have been called in question. But comparison of the external form and of the anatomy of the Calamarians leaves no doubt of the natural affinity of these plants with *Equisetum* : and it follows that their strobili are also comparable with those of modern Horsetails. The constitution of most of these shows the two types of appendage associated together, viz., sporangiophores comparable with those of *Equisetum*, and bract-leaves similar in arrangement and nature to the foliage leaves (Figs. 127-130). This suggests that while there are two quite distinct constituents of the cones of most of the Calamarians, the cones of *Equisetum* and of *Archaeocalamites* possess only

one, viz., the sporangiophore. This suggestion is based primarily upon those Calamarian strobili in which each leaf-whorl is regularly succeeded by a whorl of sporangiophores (Fig. 128). In the strobili the bracts of successive whorls show a radial alternation, as in the vegetative shoot, and it seems natural to suppose that they accordingly correspond to the ordinary succession of them in the vegetative region. But in addition to the sterile bracts the sporangiophores are present, and their presence does not disturb the alternate succession of the leaves. If the sporangiophores were rightly regarded as leaves it might be anticipated that the alternate succession of the sterile leaves would be disturbed where the sporangiophores intervene between their whorls, but it is not. Again, though the number of the sporangiophores is frequently half that of the sterile leaves, that numerical relation is not strictly maintained, while their disposition in vertical, non-alternating series is on a plan apart from that of the alternating whorls of sterile leaves. Their position on the internode also, sometimes at the base, sometimes at the upper limit, often in the middle, again shows their independence of the sterile leaves (compare Figs. 128-130). These facts together point to their being structures of a different nature from the bracts of the strobilus.

It may be asked how this non-phyllome theory of the sporangiophores is compatible with the facts in *Equisetum*, in which the annulus has usually been accepted as a transition from the foliage-whorls to the sporangiophores (Fig. 143). It is true the annulus lies at the boundary between the sterile and fertile regions, and that in *Equisetum* no vestiges of leaf-whorls are found higher up among the sporangiophores. Von Goebel has pointed out an obvious protective use for the annulus, which would sufficiently account for its constancy and limited size in the genus. A comparison of other types of Equisetineous strobili affords the following explanation of the *Equisetum* strobilus in terms of the fossils. In the genus *Archaeocalamites* (*Bornia*) Renault describes for *B. radiata*, Brongn., how the fructifications are simple, or interrupted in their length by verticils of leaves, which render the spike itself, so to speak, articulated and of very variable length. The condition of these spikes is then different in proportion, rather than in essential points from that described for *Phyllothea* (Fig. 122), and so curiously reproduced in the abnormal *Equiseta* described above (Fig. 121). This again differs from *Calamostachys* mainly in the fact that here only a single whorl of the sporangiophores intervenes between the successive leaf-whorls (Fig. 128). The tracts which bear the sporangia being thus variable, it would appear that the *Equisetum*-type is merely an extreme case, in which the whole series of sporangiophores forming the terminal strobilus are collectively above the last leaf-sheath, and that last leaf-sheath is of a reduced type, and appears as the annulus (Figs. 120, 139, 143).

It is obvious that in the present state of our knowledge the case is not proved either for the phyllome-theory of the sporangiophore in the Equis-

tales, which is out of harmony with the known facts in the fossils ; or for the non-phyllome theory, which is certainly a less obvious explanation of the simple strobilus of *Equisetum*. But the balance of evidence is strongly in favour of the latter, as without undue pressure it covers the whole area of facts, including those relating to the fossil Equisetales.

These paragraphs, quoted from *The Origin of a Land Flora* (pp. 383-4), present the problem as it stood in 1908, when the book was published. Since then there have been advances both in relative fact and in argument. These have been admirably summarised by Lady Isabel Browne (*Ann. of Bot.*, xli., 1927, p. 301), and a Theory of the Morphology of the Calamarian Cone has been formulated by her in terms which do not differ materially from the view conveyed in a less definite manner above. But the position has been stated with much greater decisiveness, and consolidated by reference to a widened field of fact, of which she has special knowledge. The present theory then is *that the bractless type of cone in Equisetum, consisting of successive more or less irregular whorls of sporangiophores—though perhaps interrupted at intervals by whorls of ordinary leaves—was primitive ; that eventually microphylls were intercalated regularly, in such forms as Calamostachys and Palaeostachya, between the whorls of sporangiophores, and that they assumed a protective function towards the developing sporangia.*

In support of this theory the greater antiquity of the bractless cones is quoted (e.g., *Archaeocalamites*)—notwithstanding that this is the sole type of Equisetoid cone which has persisted to the present day. It is further pointed out that, as far back as we can trace the Equisetales, their leaves and sporangiophores have been strikingly different. No Calamarian cone is known in which the bracts show any sign of having arisen from the sporangiophores. Further, the theory finds very strong support in the independence of the fertile and sterile whorls in point of number and of position of their parts. In particular, the rule in well ascertained cases that the bracts of successive sterile whorls are alternate with one another, while the sporangiophores of the fertile verticils are superposed, shows that these organs were inserted on the axis on two independent systems ; moreover, they frequently varied independently in number.

Lastly, there is evidence in the more elaborate cones of fission, whether of the sporangiophores or of the bracts ; and that this, when it occurs, commonly involves both. Herein there is a parallel with what is seen in *Cheirostrobilus*.¹

¹ For a detailed analysis of the relative positions of sporangiophores and bracts, and their respective branchings in the "Articulatales" at large, reference may be made to Hirmer (*Handbuch der Paläobotanik*, pp. 376-474). His Fig. 563 gives a diagrammatic representation of the form and subdivision of the *sporophyll-unit* (Sporophyll-einheit), as seen in Articulate plants generally, but always from the point of view that bract and sporangiophore are parts respectively of that unit. This conception is not in harmony with the view here entertained : which is that they are parts of distinct history and nature, and that they may be in juxtaposition, but are not necessarily so.

Other views as to the morphology of the cone of the Equisetales have been advanced : they have been considered and critically evaluated, with ample references to the literature, in Lady I. Browne's paper of 1927. The discussion is there conducted by comparisons for the most part within the Articulate Series. But in conclusion the authoress points out how greatly the hypothesis, of the relative primitiveness of the bractless cone in the Equisetales, has been strengthened by the discovery of the fossils distinguished as the Proto-articulatae, occurring in the early Devonian Period. If the balance of evidence was strongly in favour of a non-phyllome theory of the sporangiophore in 1908 it has gained greatly in strength both from fact and from argument since that time. Its acceptance forms an initial step towards the adoption of the bractless cone as a general feature of the primitive Equisetales. The advent of bracts associated with the sporangiophores would not affect the morphological character of either type of appendage.

The fertile shoots of the Equisetales may thus be held, on grounds of comparison with the Calamarians, to be composite, involving two classes of appendages borne upon the central axis. The evolutionary relations of these may be interpreted by reference to the subaerial shoot of Asteroxylon, where two distinct regions are seen bearing appendages (Frontispiece). The *Thursophyton*-region of its shoot is sterile, and bears microphylls : the *Hostimella*-region is leafless, but it bears distal sporangia on its forking branches. It is suggested that the *Thursophyton*-region is correlative to the sterile shoot of the Equisetales, though in the former the leaves are alternate and in the latter whorled. The *Hostimella*-region is the correlative of the bractless cone of *Equisetum* or of *Archaeocalamites*, though in the former the branching is diffuse, in the latter compact. If the *Hostimella*-type of shoot were condensed so that the branchlets bearing distal sporangia were compacted together, the result might be something in the nature of the sporangiophores of *Sphenophyllum* or of *Equisetum*. The theory here advanced is that this is their real nature, and that the bractless cone of *Equisetum* is the correlative of a main axis bearing condensed fertile twigs, while the bracts, of the nature of *Thursophyton*-leaves, originally stopped short at the base of the fertile region ; but that in a derivative state they invaded the fertile region, either as seen in the occasional whorls of *Phyllothea* and of certain abnormal specimens of *Equisetum* (Figs. 121, 122), or, as in most Calamarians, intervening regularly between the successive whorls of sporangiophores. The annulus of *Equisetum* would then represent a last whorl of sterile microphylls before the fertile cone is reached. This origin of the appendages would be compatible with the otherwise inexplicable fact that, while the whorls of bracts in the cone of *Calamostachys* alternate, those of the numerically different sporangiophores do not. This statement of opinion for the Equisetales must suffice for the present ; the

whole question of strobiloid structure will be taken up again in a later Chapter (XXIX).

Finally, whether in the vegetative region as the toothed leaf-sheaths, or in the strobilus as the bracts, the foliar organs of the Equisetales are held to be of the nature of *Microphylls* or *Thursophyton*-leaves. This accords with the appearance of the first leaf-sheaths laterally below the stem-apex of the embryo, and equally with the origin of the later leaves: both normally sterile, and ranking as enations of lateral, and not of distal origin.

CHAPTER XI

LYCOPODIALES

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GENERAL MORPHOLOGY

The Lycopodiales, or Club-Mosses, constitute a well-defined Class of plants with a history extending from the Palaeozoic Period through intermediate Ages to the present day. In early times it was represented by many dendroid types, as well as by those of smaller size, but now it is represented only by relatively small living plants. These comprise many species of the genera *Lycopodium* and *Selaginella*, with a wide geographical spread; also two highly specialised genera of more limited habitat, viz., *Phylloglossum* and *Isoetes*. The structure of the sporophyte of them all is so far conformable to a general underlying scheme that the phylum constitutes a naturally circumscribed Class. The Lycopodiales are essentially microphyllous forms, and though in some instances the leaves may be of considerable size the axis is as a rule the dominant feature. The shoot is occasionally unbranched, but it commonly undergoes repeated dichotomous forking, sometimes with transition to the monopodial type. The leaves are, with very few and early exceptions, simple in form, and in the adult they are inserted laterally upon it in acropetal order, sometimes in regular whorls, but more frequently according to some spiral scheme. The plant thus constructed as regards the subaerial parts is fixed and supported in the soil by adventitious roots (Fig. 148). In the living species these usually spring directly from the lower regions of the stem, but in the larger dendroid types they were borne on basal "Stigmarian" trunks, which spread with wide dichotomy in the soil (Fig. 159), and limited or vestigial remains of these may be seen in the Triassic fossil *Pleuromeia* (Fig. 160), or in the living *Isoetes* (Fig. 164). Perhaps the enigmatic "rhizophores" of many species of *Selaginella* are parts of a like nature, a point to be discussed later (Fig. 158).

The fructification is the most characteristic feature of the Class. The

sporangia are borne singly, each subtended by a sporophyll of simple form. The relationship of these parts is such that the median planes of sporangium and of sporophyll coincide, though the form of either part may vary, while the insertion of the short sporangial stalk may be either upon the axis or upon the leaf-base. The fertile regions where these parts are borne are sometimes little differentiated from the sterile regions where they are absent, and those regions may alternate successively, as they do in *Lycopodium Selago* (Fig. 148). On the other hand the fertile regions may be differentiated as specific cones or strobili, borne distally. Lastly, the shoot-system thus constituted may be radially developed, as it was in most of the fossils, and still is in many living Lycopods; or it may be dorsiventral as in some species of *Lycopodium*, and in most of the larger living species of *Selaginella*: in which case the habit of a whole shoot-system may be not unlike that of a Fern frond (Fig. 157).

The Lycopodiales are divided into two distinct series, according to the presence or absence of a "ligule," which is a minute scale arising from a depressed pit in the upper surface of each leaf, near to its base. The *ELIGULATAE* in which that organ is absent include the Lycopodiaceae with their living genera *Lycopodium* and *Phylloglossum*; also certain of the smaller fossils designated *Lycopodites* may have been eligulate. The *LIGULATAE* include the living genera *Selaginella* and *Isoetes*, together with the fossil Lepidodendraceae and Sigillariaceae.

A. ELIGULATAE

The genus *Lycopodium*, including about a hundred species, comprises most of the living eligulate Club-Mosses. Many of them are shrubby ground-living plants, but others have a trailing or even an epiphytic habit, especially

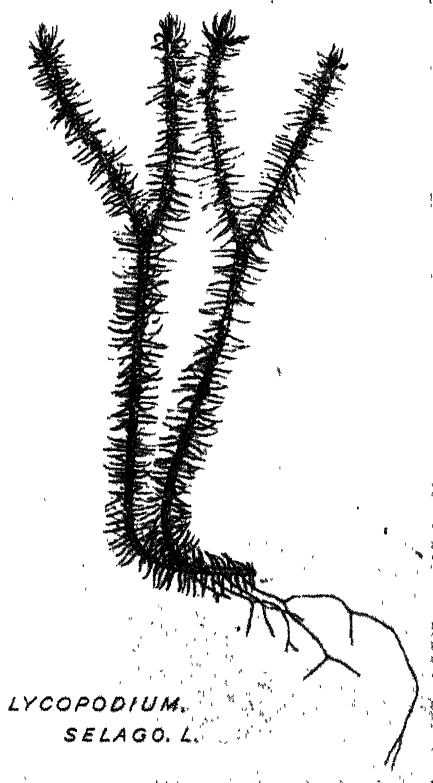
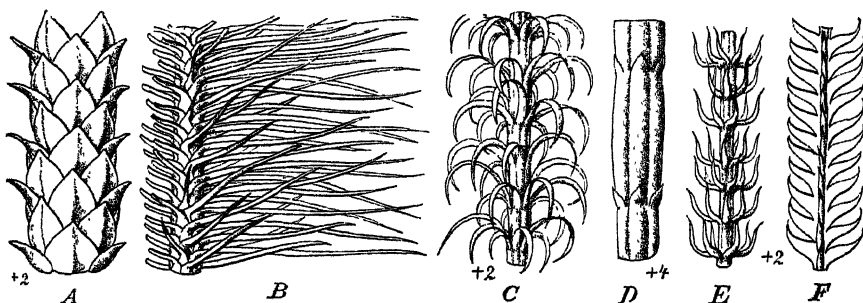


FIG. 148.

Whole plant of *Lycopodium Selago*, showing ascending and upright habit, as developed when growing protected by Heather. The equal dichotomy, and the alternating sterile and fertile zones are seen, and the forking of the roots. Distally bulbils are borne. Reduced.

in the tropics, and a few are straggling climbers. The former have radial shoots, but the latter tend towards dorsiventrality. The leaves are small and vary in form and arrangement. Sometimes they are whorled, but sometimes there is a spiral scheme, which is liable to be irregular and interrupted (Fig. 148 *bis*). Spring¹ distinguished two main sections of the genus: the first including those with sporangia scattered over the length of the shoot, the second including those with the sporangia associated in definite cones. The former section was again subdivided according as the leaves were all alike, or as a distinction appeared between sterile and fertile leaves; the latter section according as the shoot was developed radially or dorsiventrally. The details of Spring's scheme have since been modified, but the principle remains the same in the classifications of the present day: it is to arrange

FIG. 148 *bis*.

Shoots of several species of *Lycopodium* to show the form and arrangement of the leaves. *A*=*L. rufescens*, Hook. $\times 2$. *B*=*L. manducanum*, Raddi. Natural size. *C*=*L. reflexum*, Lam. $\times 2$. *D*=*L. casuarinoides*, Spring: part of a terminal branch of an old plant. $\times 4$. *E*=*L. cernuum*, L. $\times 2$. *F*=*L. volubile*, Forst, is dorsiventral, and is here seen from above. $\times 2$. (From Engler and Prantl.)

the genus along lines which clearly indicate a progressive differentiation and specialisation of sterile and fertile tracts. Such an arrangement naturally harmonises with evolutionary theory. The species which Spring placed first of all was *L. Selago*; and though this may not be actually the most elementary living species in the genus, still it is the best known of those which show a low degree of differentiation.

The plant of *L. Selago* is shrubby, with dichotomously branched axes, bearing numerous leaves of approximately equal size and simple form (Fig. 148). There is usually a sterile region at the base of the plant: this is followed by the well-known alternating sterile and fertile zones, the length of which corresponds with a high degree of exactitude on the several branches. They are stated to be determined by successive seasons, the middle region of each year's increment of growth being fertile. These zones are not definitely marked by any distinction of the leaves themselves, but by the presence or absence of sporangia: nor are they strictly delimited in this respect, for occasionally a single sporangium may be found in an otherwise

¹ *Monographie des Lycopodiacees*, 1841.

sterile region. About the limits of these zones sporangia of smaller size may be found, which sometimes remain closed when all those near them have dehisced. The condition thus seen in *L. Selago* is shared in more or less complete degree by about 40 living species, which constitute the section

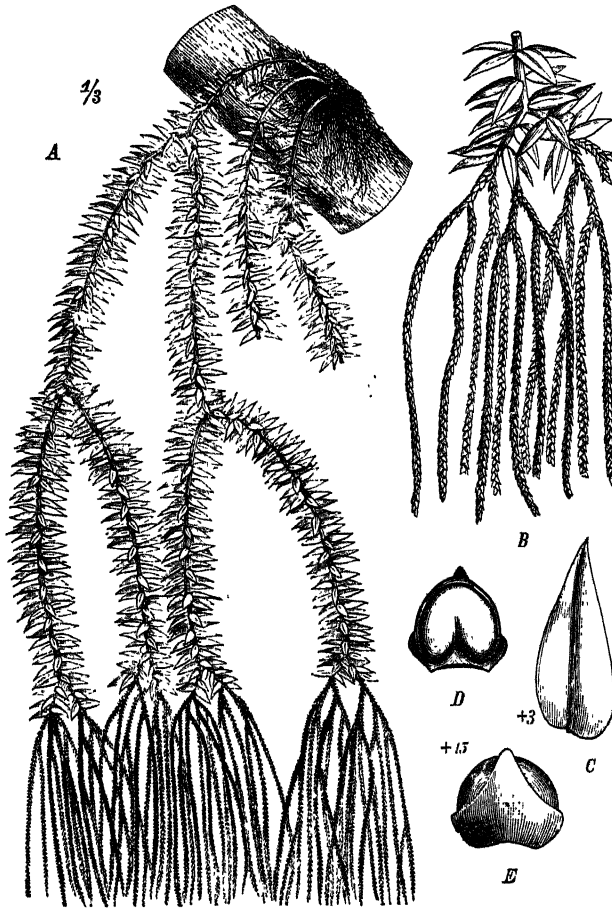


FIG. 149.

L. Phlegmaria, L. A, figure showing the habit of the whole plant; reduced to $\frac{4}{3}$. B, end of a branch, natural size. C, a sterile leaf somewhat enlarged. D, a sporophyll seen from above, enlarged. E, a sporophyll seen from below, enlarged. (From Engler and Prantl. *Natürl. Pflanzenfam.*)

Selago: they are mostly ground-growing plants. An examination of them shows that while many of them have, like *L. Selago*, a sterile basal region of considerable length, still in certain species (*L. compactum*, Hook., and *L. Trencilla*, Sodiro) sporangia have been found in the leaf-axils down to the base of the mature plant. Unfortunately these species are unknown in the embryonic state, so that it is impossible to tell how early in the individual

life the formation of sporangia actually begins. The incomplete differentiation of the sterile and fertile zones, together with the occurrence of incompletely developed sporangia at the limits of the zones, and the very uniform character of the leaves whether sterile or fertile, have their direct bearing on any theory of origin of the Lycopod strobilus.

Some ten other species were grouped by Baker under the heading *Sub-Selago*, and are characterised by having the sterile leaves a little different from the fertile, but passing into them gradually, while the sporangia are aggregated into indistinct terminal spikes. All the species thus grouped have a sterile basal region : above this follows a recurrence of sterile and fertile zones, as in § *Selago* (*L. Dalhousiae* *nummum*). There is thus a close similarity to what is seen in the *Selago* group, but with gradually increasing definition of the strobilus from the lower vegetative region.

In the *Phlegmaria* group, which includes about eighteen species of epiphytic character, the spikes are slender, and dichotomously forked, with sporophylls as a rule very different in size from the foliage leaves (Fig. 149). Occasionally sporangia may be found in the vegetative region subtended by leaves of the foliage type (*L. varium*) ; while, on the other hand, leaves of the sporophyll type may develop no sporangia (*L. subulatum*, *Phlegmaria*). There may occasionally be alternating sterile and fertile zones (*L. nummularifolium*). Transitions from the fertile strobilus to the larger-leaved foliage shoot are frequent (*L. nummularifolium*, *subulatum*, *ophioglossoides*, *pinifolium*, *Phlegmaria*). Thus the differentiation of the strobilus is one of external form rather than a rigid difference of intimate character.

The above groups, including fully one half of the living species of *Lycopodium*, are now associated together under the sub-genus *Urostachya* ; the characters assigned are not only those of the distribution of the sterile and fertile zones, but extend also to other features. The branching of the axis is almost, or entirely, absent in the simplest of the upright forms ; in the trailing or pendulous forms it is more frequent. It is of the dichotomous type, and usually in planes successively at right angles. The roots arise primarily from the basal region of the axis ; in no case is there a creeping monopodial axis, with adventitious roots arising along its whole length. In about half of the species there is no formal distinction of sporophylls from the foliage leaves : where such a distinction exists the sporophylls still have a green colour, and as a rule an entire margin. The spores have a pitted surface, without external processes. These general characters indicate a natural grouping of species which are certainly the simpler living representatives of the Lycopod type.

The second sub-genus, designated *Rhopalostachya*, includes the remaining species which are more differentiated than the first in many of their characters. The branching of the axis is only dichotomous in the younger parts, and becomes monopodial later, often with a well-marked main axis. All the species are ground-growing ; a few are climbers. The upright species are freely branched, as in *L. cernuum* (Fig. 150). In the creeping species the recumbent axis gives off upright branches, and is attached to the soil by successive adventitious roots. The fertile strobili are for the most part definitely marked off from the sterile region, and are often carried upon elongated stalks, which

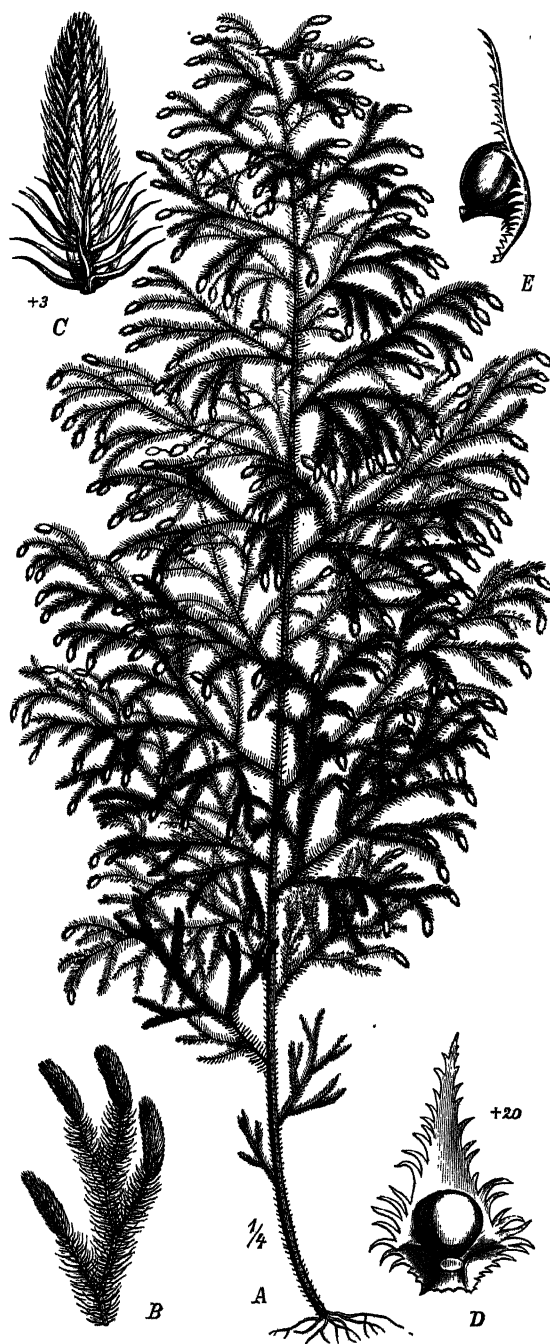


FIG. 150.

Lycopodium cernuum, L., var. *Eichleri*, Glaz. A, general habit ($\frac{1}{4}$ natural size); B, end of a branch (natural size); C, strobilus ($\times 3$); D, sporophyll seen from above; E, ditto, from the side ($\times 20$). (After Pritzl, in Engler and Prantl, *Nat. Pflanzen.*)

bear minute scale-leaves (Fig. 151). The differentiation of the sterile and fertile leaves is constant; the sporophylls are pale, often chaffy scales, with toothed, ciliate margin (Fig. 150 *D, E*), while the spores bear reticulate flanges or prickles on their outer wall. These characters collectively mark off *Rhopalostachya* as more differentiated than *Urostachya*. But it includes some species which approach the latter; thus the three species associated as the *inundatum* group show only slight differentiation of the strobilus from the vegetative shoot, while abortive sporangia are found at the base in *L. inundatum*. *L. Drummondii* even approaches *L. Selago* in its alternation of successive and fertile zones. In the rest, however, the definition is more exact, and is strictly maintained. The same is the case in the species associated as the group of *L. clavatum*, which are terrestrial trailing species, with well-defined strobili. Here the intercalation of a peduncle, with small distant scales, between the larger-leaved foliage shoot and the definite strobilus is indicated (Fig. 151). The biological importance of it in ground-growing forms is readily understood.

Finally, the dorsiventral species, previously grouped as the sub-genus *Diphasium*, are now distributed according to their obvious affinities; the dorsiventral character of their vegetative shoot being held as a secondary adaptation: the strobilus, however, remains as clearly defined as in the more advanced representatives of the sub-genus *Rhopalostachya*, and does not share in the dorsiventral development.

A comparison of the living species of *Lycopodium* thus appears to demonstrate a progression from a less differentiated to a more differentiated state. In the simplest forms the whole of the unbranched or sparsely-branched shoot is practically a fertile strobilus, which serves the double purpose of assimilation and of spore-production. By gradual steps the living species suggest how the two functions became separated topographically.

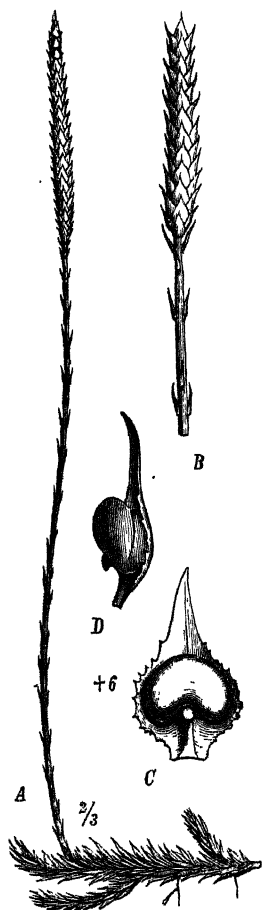


FIG. 151.

L. carolinianum, L. A, shows the general habit; about $\frac{2}{3}$ natural size. B, strobilus, natural size. C, sporophyll seen from above, $\times 6$. D, the same from the side, $\times 6$. (After Engler and Prantl.)

The only other living genus of eligulate Lycopods is the monotypic *Phylloglossum*, long recognised as the simplest of them all. The mature plant as seen above ground consists of a tuft of almost cylindrical assimilating leaves, from the midst of which rises the simple axis terminated by the short strobilus; below ground are found two ovate storage tubers, one dating from

the preceding year and in course of exhaustion, the other in course of development as a store for the succeeding year. One or more roots attach it to the soil (Fig. 152). The lower parts of this curious little plant cannot be properly discussed till it is compared with the embryos of certain species of *Lycopodium*, for it seems to repeat in its annual growths their embryonic characters. The very short strobilus shows a similarity to the *Urostachya* rather than to the *Rhopalostachya* section of the genus: this is seen in the smooth margin of the rather fleshy sporophylls, as well as in the incomplete protection of the sporangia. It is interesting to note that transitions are occasionally found between the foliage leaves (protophylls) and the sporophylls. Fig. 153, *A*, shows a case where a single sporophyll of larger size than the normal, with a sporangium in its axil, stands isolated some way below the strobilus: thus it is intermediate both in position and in character between the two types. A small protophyll without any sporangium may also sometimes be found at the base of the pedicel. Dichotomous branching of the strobilus is sometimes seen, but it is rare: an example is shown in Fig. 153, *B*. Such features are important for comparison with *Lycopodium*, and indicate that there is a close relation between the two genera.



FIG. 153.

Philloglossum Drummondii, Kunze. *A*=a plant showing protophylls and strobilus: one sporophyll of the latter is at a distance below the rest, intercalary growth having taken place in the axis above it. $\times 3$. *B*=a plant with the strobilus branched into two unequal parts. $\times 3$.

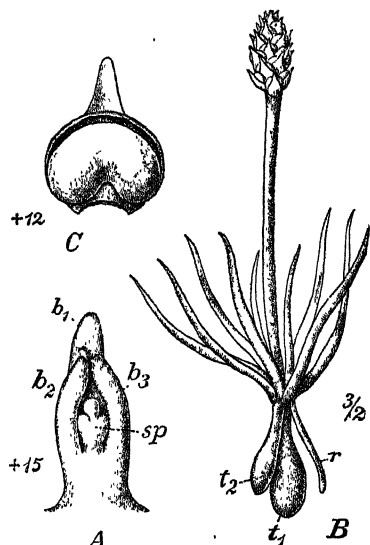


FIG. 152.

Philloglossum Drummondii, Kunze. *A*=apex of a germinated tuber; b_1, b_2, b_3 , leaves; *sp*=the young strobilus. $\times 15$. *B*=the whole plant. \times one-half. t_1 =the old tuber; t_2 =the young tuber; *r*=root. *C*=sporophyll with sporangium seen from above. $\times 12$. (After Engler and Prantl.)

Of the fossils which have been referred to a near affinity with *Lycopodium* under the name *Lycopodites*, many have been shown to find their true place elsewhere. But some at least of them show distinct Lycopodinous characters: for instance, *Lycopodites Stocki*, Kidston, from the calciferous sandstone of Dumfriesshire (Fig. 154). In habit it is like *Lycopodium Phlegmaria*, showing a terminal strobilus, with sporangia, and the sporophylls smaller than those borne by the more lax region of the shoot below. The leaves are arranged in whorls—a condition not unknown among species of the *Phlegmaria*

group. The sporangia do not appear to have been restricted to the terminal strobilus, but to have occurred also in relation to the larger foliage leaves : this is a condition which has been seen to occur in living species of

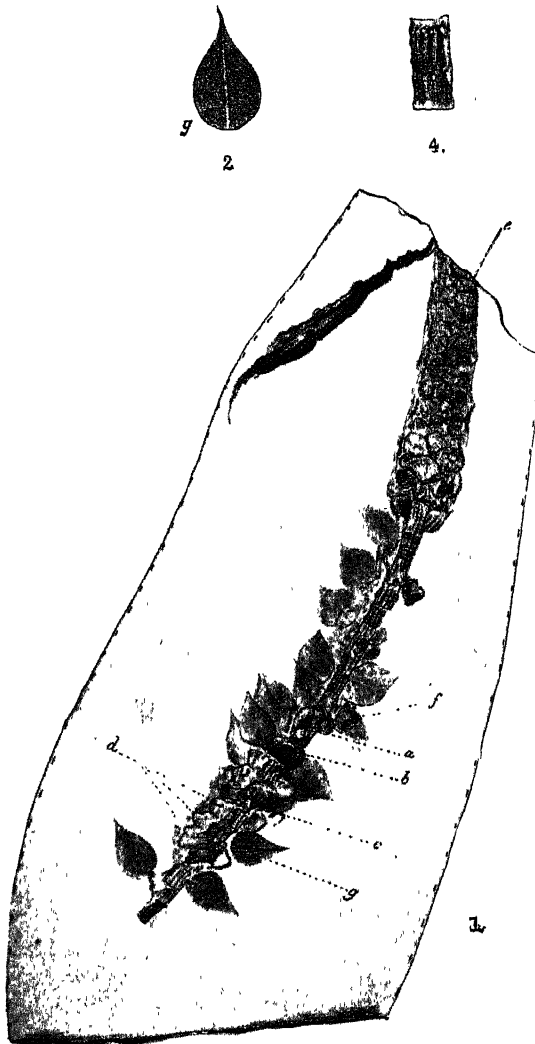


FIG. 154.

Lycopodites Stocki, Kidst. 1=specimen, natural size; a-f, sporangia; g, sporophyll. 2=sporophyll enlarged. 4=small portion of stem, enlarged, showing verticillate leaf-bases. (After Kidston.)

the group *sub-Selago*, from which the *Phlegmaria* group appear to be a specialised offset. So far from this distribution of the sporangia raising a difficulty, it seems to point to the existence in very early strata of a Lycopo-

dinous type showing characters which exist in living species, and which comparison indicates as primitive. These fossils are unfortunately rare, and in the particular case of *L. Stocki* the essential facts are based upon a single specimen.¹

In this relation *Spencerites* may also be mentioned: a fossil from the Coal Measures, known only by its cones (Scott, *l.c.*, p. 169). It is peculiar in the form of its verticillate sporophylls, each consisting of a pedicellate base bearing a distal blade with a broad fleshy base, while the ovoid sporangium is seated at the junction of stalk and blade. No ligule has been observed (see Fig. 194, p. 248). The spores are winged, and relatively large, but no evidence of heterospory has been seen. Prof. Lang compares the structure of this cone with that of *L. cernuum*; but the relations of *Spencerites* are still problematical (Lang, *Proc. R.S. Edin.*, 1908, xxviii., p. 356).

Vegetative propagation is seen in various species of *Lycopodium* by means of easily detached bulbils, which in themselves raise interesting morphological questions. They appear in *L. Selago* as buds associated with leaves and sporangia (Fig. 148). Hegelmaier (*Bot. Zeit.*, 1872, p. 775) showed that their insertion took the place of leaves in the spiral sequence; this point was confirmed by Wilson-Smith in *L. lucidulum* (*Bot. Gaz.*, 1920, p. 426). Opinions have differed as to the reading of this fact. Some hold that the bulbil represents the survival of an original dichotomy formed without relation to leaves (Strasburger, Campbell); but Wilson-Smith concludes that the bulbil is not the homologue of a branch but of a transformed leaf, retaining its position, dorsiventrality, and the foliar character of its vascular supply. Williams also holds this to be probable (*Trans. R.S. Edin.*, 1933, vol. lvii., p. 730). The formation of bulbils may perhaps best be recognised as an example of such indeterminate definition of parts as may be expected to occur in very primitive leafy plants, and especially in early stages of their individual development. The bulbil of *L. lucidulum* consists of a short stalk bearing three pairs of fleshy leaves, the first and third being in a median plane; these, which become disorganised on germination, are followed by smaller leaves closely disposed about a growing point; while one or two endogenous roots push out on germination into the soil. The apical bud soon forks, especially in *L. Selago*: and so a new plant is established.

B. LIGULATAE

The ligulate Lycopodiales resemble the eligulate in their microphyllous habit, but they differ from them in the presence of a small process—the ligule—borne on the upper surface of each leaf, near to its base; also, whereas the living Eligulatae are all homosporous, all the living Ligulatae

are heterosporous. Among the fossils heterospory is prevalent, but there are no fossil records of heterosporous eligulate types (Walton, *Proc. R.S. Edin.*, vol. li., p. 114). *Selaginella* is the preponderant living genus with over 300 species. Some few of the smallest of these are radially constructed, and may even be unbranched. But the majority show dorsiventral development, with anisophyllous leaves and profuse branching. As the result of experiment on species such as *S. sanguinolenta*, in which anisophylly is not constant but appears under the influence of external factors, it is concluded that the dorsiventrality is a phenomenon of adaptation brought about by light, and the radial type is held as the more primitive. This accords with what is seen in *Lycopodium*. Nevertheless the strobilus, with few exceptions, is isophyllous, even where the vegetative shoot is anisophyllous; this

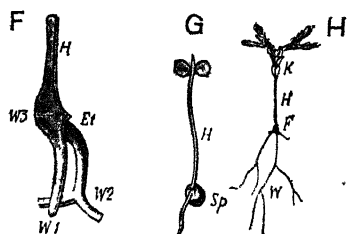


FIG. 155.

Selaginella spinulosa. G=young sporophyte with megaspore attached, showing elongated hypocotyl (H) and cotyledons K. H=sporophyte more advanced, showing dichotomy. F=base of hypocotyl with swollen knot. W=roots. H=hypocotyl. Et=suspensor (after Bruchmann). H=natural size. F, G=enlarged.

suggests that it is the more conservative part of the plant. The definition of the strobilus from the vegetative shoot is more marked in *Selaginella* than in *Lycopodium*. A condition corresponding to that of the *Selago*-group of *Lycopodium* is rare (Mitchell, *Ann. of Bot.*, 1910, p. 19). Thus the differentiation of the sporophyte of the genus as a whole corresponds to that of the more specialised types of *Lycopodium*. Imperfect sporangia have been observed at the base of the strobilus in *S. spinulosa* and *Martensii*, and isolated sporangia sometimes exist in the axils of ordinary leaves (*S. molliceps*. Mitchell). Such facts are open to the same interpretation as in *Lycopodium*. As is well known, the megasporangia and microsporangia are alike in their early stages of development, though differing later in the spores which they produce. Thus the advance to heterospory, as it is seen in *Selaginella*, accords with a higher differentiation of its vegetative organs as compared with *Lycopodium*.

Of the species with radial construction, some are unbranched; but the best known is *S. spinulosa*, which branches dichotomously: it has been specially investigated by Bruchmann, and it will be briefly described for purposes of comparison on the one hand with *Lycopodium*, and on the other with the related fossils, while the dorsiventral *Selaginellas* may be regarded as specialised offsets from some such radial type as this. The sporophyte of *S. spinulosa* is like that in other *Selaginellas* in having an elongated hypocotyl (Fig. 155), which is continuous downwards into the primary root: the hypocotyl bears two cotyledons, after which a variable number of pairs of epicotylar leaves are formed before the first branching, which is a true dichotomy. The limbs thus formed branch repeatedly, at first dichoto-

mously, but later monopodially, all the later branchings being in one plane, at right angles to that of the first dichotomy: thus two fan-like branch-systems are produced, of which certain stronger branches are fertile, the rest sterile (Fig. 156). The arrangement of the leaves of the primary axis is decussate, but on the later branches there are transitions to spiral, while in the thicker strobili the arrangement is on a complex spiral plan. The main axis terminating below in the hypocotyl remains permanent, and its base swells at the level of the suspensor to form a knot, from which alone the later

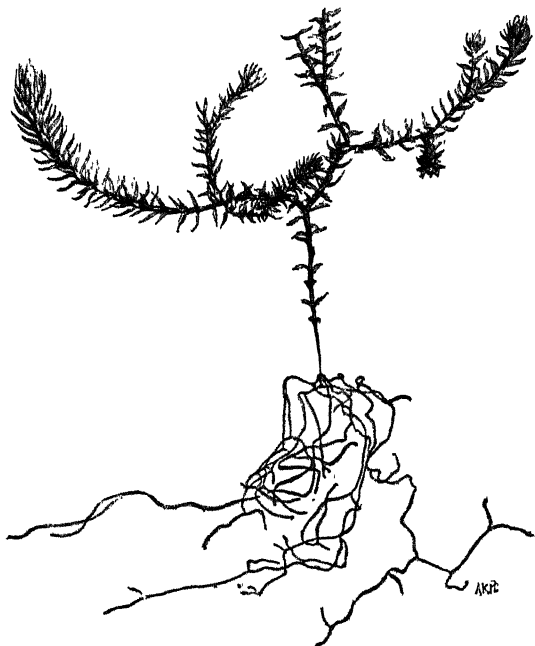


FIG. 156.

Plant of *Selaginella spinulosa*, with root-system springing from swollen knot at base of the upright hypocotyl. Natural size.

roots originate; they are formed endogenously in swellings of tissue of the knot, and burst their way outwards through the superficial tissue (Fig. 155, *F*). The whole plant of *S. spinulosa* is thus dependent upon a central source of water-supply from the base of the main axis.

Of the dorsiventral types some of the largest are caulescent, with erect stems springing from a decumbent rhizome. They are simple below and branched above in a single plane, giving a frond-like habit, and they are rooted at the base (Fig. 157). Others, including the familiar *S. Martensii*, are of ascending habit, not rhizomatous, with an espalier-like shoot (Fig. 158). In either case the branching is based upon dichotomy, with more or less marked dichopodial development. The small and simple leaves are disposed

in four longitudinal rows, those on the lower flanks being larger, those on the obliquely upward flanks being smaller. But in the fertile cones all the

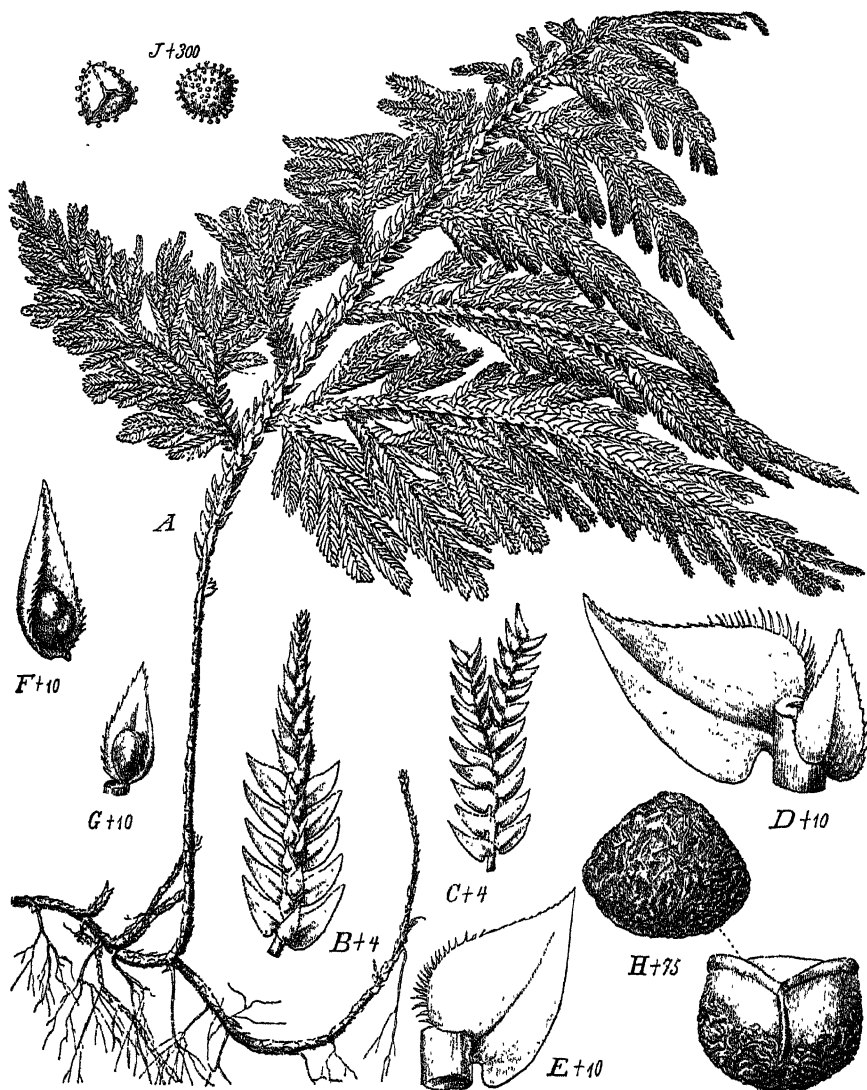


FIG. 157.

Selaginella umbrosa, Lemaire. A, habit of plant, natural size. B, terminal twig with strobilus, seen from illuminated side. C, same from shade-side. D, twig with dorsal and ventral leaves, seen from illuminated side. E, from shade-side. F, sporophyll with megasporangium. G, sporophyll with microsporangium. H, megaspores. J, microspores. (After Hieronymus, from E. and P., *Naturl. Pflanzenfam.*)

bracts are as a rule equal. The roots are not borne directly upon the axis, but they arise from "rhizophores"; one or two of these peculiar organs may

spring from any forking of the stem; their origin may be traced to a persistent meristem lying in the angle of the dichotomy. This meristem may at times, and particularly at the distal branchings, give rise to a middle-shoot in such a species as *S. grandis*; but at the basal branchings it divides into two rhizophore-rudiments. One or both of these may grow into a cylindrical organ which dichotomises, but it is not itself a root: roots arise endogenously from its tip. The rhizophore of *Selaginella* may be held as an organ standing between root and shoot: in fact a part of indifferent nature, arising in a relatively primitive organism to meet a certain need, and not referable in origin to either category (Williams, *Trans. R.S. Edin.*, vol. lvii., p. 1).

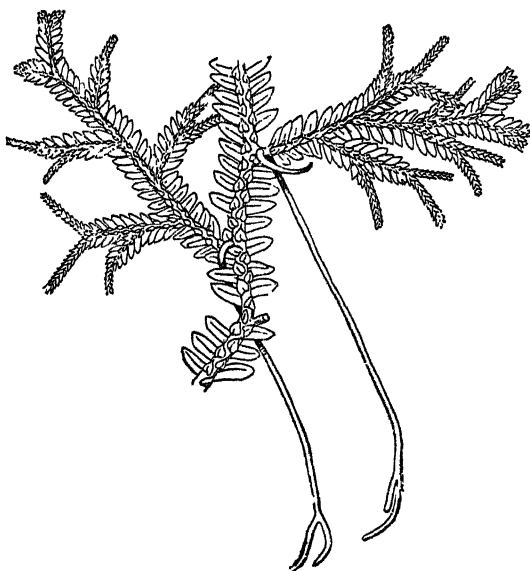


FIG. 158.

Part of the shoot of *Selaginella Martensii*, showing its "cespiti-
form" habit, and unequal microphylls. It is seen from above, and forking rhizophores are directed downwards.
Natural size. (After Goebel, from Strasburger.)

Rhizophores are absent from *S. spinulosa*, which is centrally rooted (Fig. 156). This together with its radial shoot may be held to indicate its primitive nature.

Some of the largest Palaeozoic fossils are clearly Ligulate Lycopods. But the fossil Ligulates were not all large. There is evidence that small organisms, corresponding in habit to the heterophyllous *Selaginellas*, existed also in early geological times. The fossil from the Upper Coal Measures, described as *Selaginellites Gutbieri*, Göpp, can hardly have been anything else. *Selaginellites primævus*, Goldenberg, from the Westphalian Middle Coal Measures, though it shows no distinctly Selaginelloid shoot, has heterosporous sporangia, with megaspores sometimes more numerous than four in each sporangium. A

similar condition has been described by Zeiller¹ in a plant from Blanzky, named by him *Selaginellites Suissei*, where the number of megaspores was found to be 16 to 24. In these cases the reduction in number of the spores as a consequence of heterospory appears to have proceeded less far than in most modern *Selaginellas*. But, on the other hand, the carboniferous plant described by Bertrand as *Miadesmia* corresponds in structure, as well as in the heterophyllous arrangement of the leaves and in the presence of a ligule, to *Selaginella*, while it appears to have progressed towards a seed-like fructification. The minute species *Miadesmia membranacea*, Bertrand, has been directly compared with *Selaginella spinulosa* by Miss Benson,² in respect of characters other

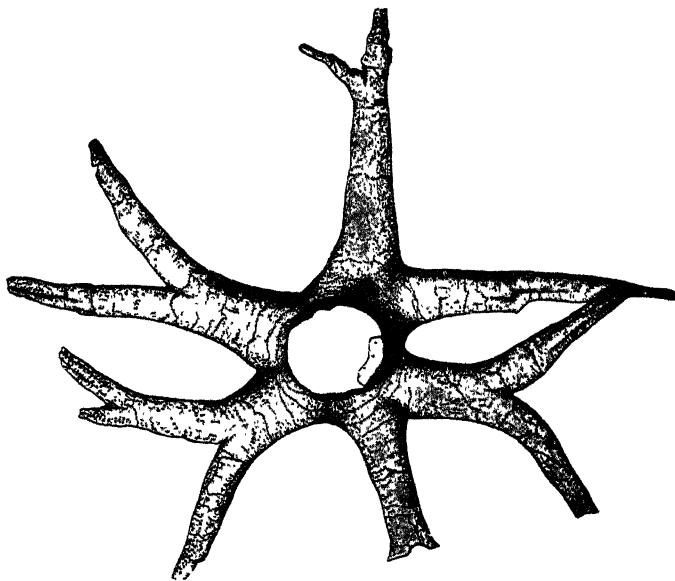


FIG. 159.
Ground plan of a Tree-stump with *Stigmara*-trunks. One-sixtieth the natural size.
(After Potonié.)

than the seed-like structure borne by the megasporophyll. A well authenticated case is that of *Selaginellites Dawsoni*, Sew., from the Wealden of Sussex: its habit was like *Selaginella rupestris*, and the megaspores and microspores have been delineated by Seward (*New Phyt.*, xii., p. 85). So far as it goes, then, the evidence from the fossils favours the conclusion that small plants resembling *Selaginella* existed very early, and that even the more specialised heterophyllous type of *Selaginella* dates at least from the Carboniferous period, while a seed-like habit had already been established at that time.

The dendroid Lycopodiales are among the earliest known fossils, dating from the Lower Devonian period to the Trias. They include the families

¹ *Comptes Rendus*, April 17, 1900.

² *Proc. Roy. Soc.*, Series B, vol. lxxix, p. 473.

of the Lepidodendraceae, Bothrodendraceae, Sigillariaceae, and Pleuromeiaceae. Underlying the differences of detail according to which these families are distinguished there is a general unity of morphological plan: the essential features of it are as follows. The main axis was upright, rising in some cases to a height of 100 feet. It was bulky relatively to the numerous simple leaves which it bore; it branched upwards in a dichotomous manner, in most cases profusely; in some of the Sigillariaceae, however, and in *Pleuromeia* branching may be entirely absent. The development of the branches of the dichotomy were in various cases either equal or unequal, a fact which leads to differences of habit, as is the case in *Lycopodium* or *Selaginella*. The axis was fixed in the soil by a shallow and broadly spreading system of Stigmarian trunks (Fig. 159). In *Lepidodendron* the main Stigmarian trunks usually numbered four, which bifurcated repeatedly, thus forming a widely spreading system: from these the rootlets radiated in all directions, developing to a length of a foot or more, and themselves also showing dichotomous branching. The underground system was thus proportional to that above ground. In the Sigillariaceae

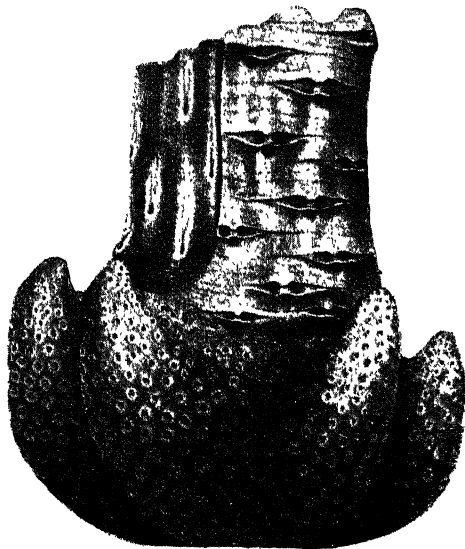


FIG. 160.

Pleuromeia Sternbergi. Swollen base of stem with root-scars, and showing part of the aerial stem, with the epidermis and leaf-scars on the right, and on the left the sub-epidermal sculpture. (After Bischof, from Engler and Prantl.) Two-thirds natural size.

similar trunks are found, but it seems doubtful whether they retained the same constancy of initial type as in *Lepidodendron*. In *Pleuromeia* the base of the upright unbranched stock swells into a tuberous body, which is very *Stigmaria*-like in the fact that it is covered by root-scars, while it extends into four blunt processes corresponding in position and character to Stigmarian trunks, though much shorter (Fig. 160). It would seem probable that in this relatively late Triassic fossil (which is unfortunately known only in the form of casts, not structurally), a simple representative of the Lepidodendroid basal region is correctly recognised. In all of the dendroid forms the Stigmarian trunk appears to have been present, as a basis for the roots; but the latter were not restricted to that position; Potonié shows how the scars of their insertion may be

sometimes found on the leaf-bearing axes also, associated with the leaf-scars.¹

The leaves of the fossil Ligulatae were sometimes of considerable size, but of simple form, and unbranched, except for certain fossils of Devonian age, such as *Protolepidodendron* and *Duisbergia*, where they forked distally (Kräusel and Weyland, *Beitr. d. Kenntn. d. Devonflora.*, 1929, Plate 13). The leaves expanded at the base into the well-known cushions, which in many forms occupy the whole external surface of the axis: this

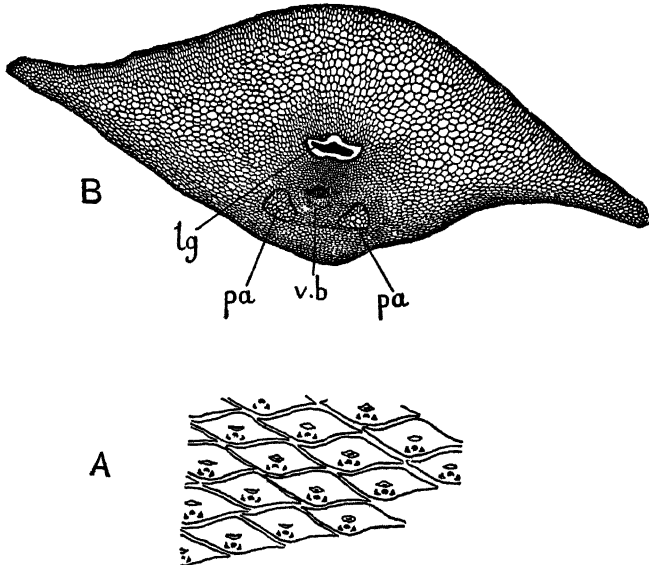


FIG. 161.

Lepidophloios, sp. A=tangential section from the outside of a stem, passing through the leaf-bases, and showing their characteristic form, slightly enlarged. B=a single leaf-base, to show details; vb=collateral vascular bundle; pa=the two parichnos-strands; lg=ligule in its pit. $\times 10$. Will. Coll., 1974A. (After Scott.)

corresponds to what is seen among the living Lycopods. On the upper surface of the leaf, near its base, the ligule is seated: it appears to have been a constant feature in the dendroid Lycopodiales, and the occurrence of it links them rather with *Selaginella* than with *Lycopodium*. It was often seated in a deep pit—as it is in some living *Selaginellas*—and this pit persists as a marked feature in the neighbourhood of the leaf-scars, whenever the cast of a stem-surface is well preserved (Fig. 161).

The vegetative region appears to have been, as a rule, purely vegetative, and the sporangia are restricted to well-defined cones or strobili, similar in their general characters, as also in their clear definition, to those of the more

¹ *Lehrbuch der Pflanzenpalaeontologie*, p. 212, Fig. 215. See also Mägdefrau, *Bot. Centralbl.*, Bd. xlviii., Abth. ii., Heft i., 1931.

differentiated types of *Lycopodium*, or to those of *Selaginella*. The structure of the strobilus is essentially the same as that of the vegetative shoot, excepting in the presence of the sporangia. These are of very large size, and are commonly extended radially outwards from the axis, a basal region being interposed between the axis and the ligule: the latter then appears on the upper surface of the sporophyll, beyond the distal limit of the sporangium (Fig. 162). In *Lepidodendron* the cones thus constructed were borne on the ends of the ordinary branches; but in *Sigillaria* they appear to have arisen laterally upon the main axis, from which after maturity they were deciduous, and each was borne upon an elongated pedicel covered with acicular bracts,

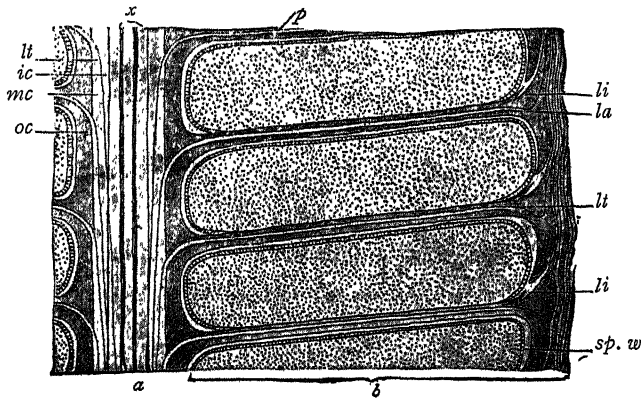


FIG. 162.

Lepidostrobus. Diagram showing axis and sporophylls in radial section. *a*=axis of strobilus; *b*=sporophylls and sporangia; *x*=stele; *ic*=inner cortex; *mc*=middle cortex; *oc*=outer cortex; *p*=pedicel; *la*=lamina of sporophyll; *li*=ligule; *lt*=leaf-trace; *sp. w*=wall of sporangium. (Enlarged after Maslen, from Scott, *Studies in Fossil Botany*.)

while the cone itself showed a construction essentially similar to that of a small *Lepidodendron*.

Though the type with a definite cone marked off from the sterile region was usual for the fossil Lycopodiales, it was not universal. In the imperfectly known plant, *Pleuromeia* from the Trias, the whole main axis seems to have been a strobilus (Fig. 163), borne upon a Stigmarian base (compare Fig. 160). But a more interesting example, from the Westphalian series (Middle Coal Measures) is that of *Pinakodendron musivum*, Weiss, specimens of which were discovered by M. Hector Delteure at Mariemont in Belgium. This large Lycopod bore its sporangia associated with the leaves of certain portions of the stem, without any cone-formation, or alteration of the form or disposition of the leaves which bear them: the fertile and sterile portions are distinguished only by the presence or absence of sporangia. It is, in fact, a representative of the "*Selago*" type, but of dendroid dimensions. These and other examples show that the "*Selago*" condition dates back to the Primary Rocks.

There can be no question of the Lycopodinous affinity of the fossils thus described in their general morphology. We shall then enquire where the nearest correspondence lies between them and living forms. They are of plainly related for the most part to the Ligulate Lycopodiales, and, being a radial type of shoot, and usually if not always heterosporous, the correspondence is nearer to the radial than to the dorsiventral species of *Selaginella* :

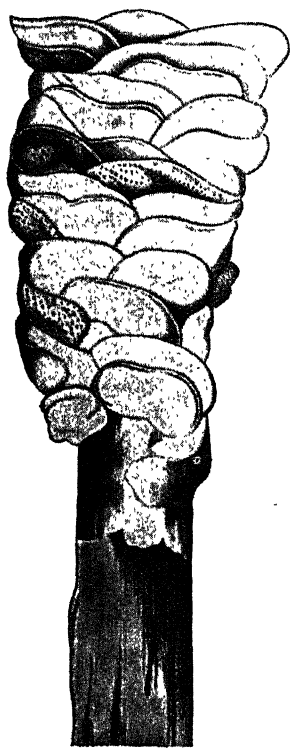


FIG. 163.

Pleuromeia Sternbergi. Axis, with the lower part of the terminal strobilus. Two-thirds natural size. After Bischof. (From Engler and Prantl.)

this suggests a comparison with *S. spinulosa*, from which some interesting points emerge. In the first place, the difference of size is to be discounted : however diverse the gigantic *Lepidodendron* may seem from the minute *S. spinulosa*, the comparison really relates to the relative position and character of the parts composing the plant-body. The parts which form the shoot—axis, foliage-leaf and sporophyll, the ligule, and the sporangium—are identical in both as regards their relative positions, though differing greatly in their number and dimensions : in the dichotomous branching, and in the relation of the resulting shoots to the upright main axis they are alike, also in the dependence of the whole plant for its water-supply upon the base of the primary axis. In fact, *Selaginella spinulosa* is like a *Lepidodendron* in miniature, as regards the scheme of its construction. The comparison extends also to that curious knot which is found at the base of the main axis in *S. spinulosa* : here the origin of the roots is strictly localised : in other species they appear endogenously on indeterminate outgrowths from the axis itself. It does not seem an undue strain of comparison to suggest that in this basal knot is still to be

seen, on a minimal scale, a living representative of those larger growths known as the Stigmarian trunks. These would then be in their nature indeterminate outgrowths of the hypocotyl. It is thus possible to bring the general morphology of *Lepidodendron* into relation to that of the modern *Selaginella*, a type which there is reason to believe itself dated from the Carboniferous period.

On the other hand, there are more obvious relations between the dendroid Lycopodiales and the living genus *Isoetes* : this type has been found fossil in Tertiary rocks, and back as far as the Lower Chalk, while in the Trias

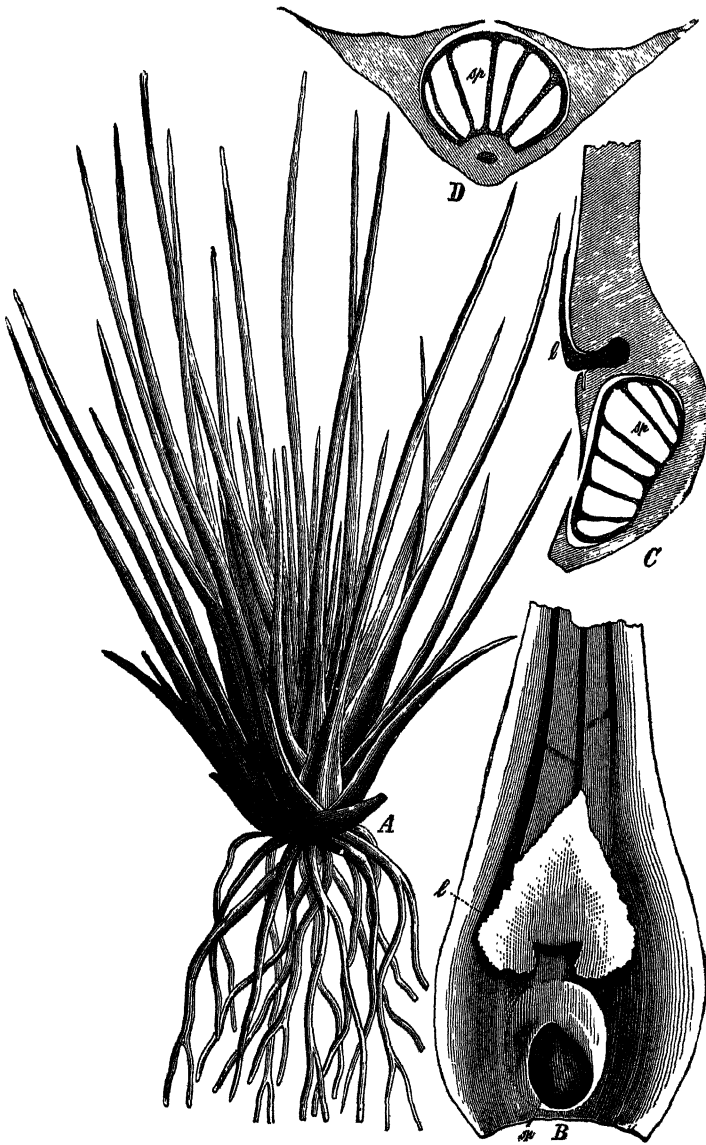


FIG. 164.

Isoetes lacustris, L. A=plant of natural size. B=base of a fertile leaf with ligule(l), and sporangium(sp) seen from above. C=longitudinal and D transverse sections of the leaf-base; sp=sporangium; l=ligule. (From Rabenhorst's *Krypt. Flora*.)

the curious fossil *Pleuromeia* is represented, which in habit serves to link *Isoetes* with the dendroid fossils; but there is no sufficient evidence of the genus *Isoetes* having itself figured among the earliest fossils.

The plant of *Isoetes* consists of a short upright axis covered by the bases of relatively large leaves (Fig. 164): the axis is usually unbranched, though bifurcation occasionally occurs, a fact that has its interest for comparison with the Lycopods.¹ The leaves are essentially of one type, with broad base and acicular upper part, while seated in a pit on the upper surface, at some little distance from the base, is the ligule: they may be either sterile or fertile, and in some species there is a difference in size, the sterile leaves being the smaller. The plant is heterosporous. Where the leaf is fertile the large cake-like sporangium lies in a depression of the leaf-surface, between the ligule and the leaf-base, that region being elongated to accommodate it (*B*); in the sterile leaves it is shorter. An examination of the sterile leaves of *I. lacustris* and of *I. echinospora* shows that sporangia in various degrees of abortion may be found upon them: in some of these spores are developed,

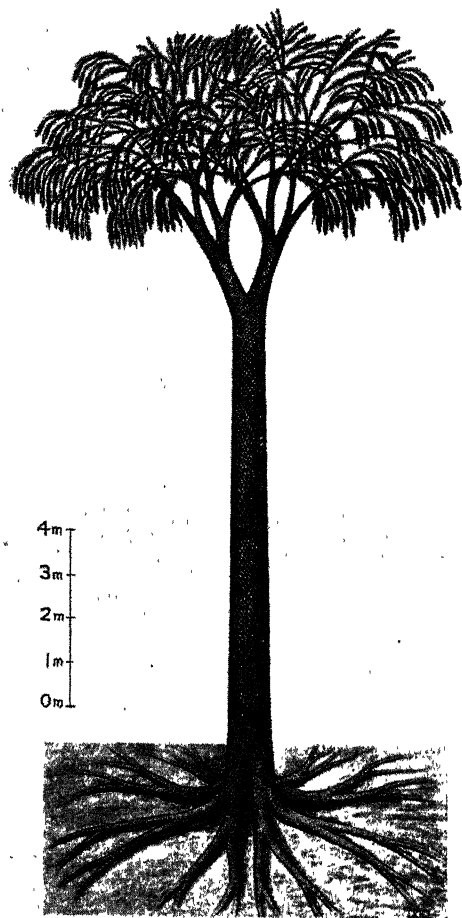


FIG. 165.

Lepidodendron of the type of *L. obovatum*, Sternberg. Reconstruction after Hirmer. The strobili are for clearness' sake represented relatively larger than they should be.

but in smaller numbers than the normal; other sporangia may remain quite small, and produce no spores. Dissections show that, in the majority of such leaves as are apparently sterile, a rudimentary sporangium is really present in a normal position. It is stated that a regular seasonal sequence is followed in the distribution of the megasporophylls, the microsporophylls,

¹ Solms Laubach, *Bot. Zeit.*, 1902, p. 179.

and the foliage leaves ; that the megasporangia are borne on the first or outermost leaves of each annual increment, then follow leaves with microsporangia, while the sterile leaves form the transition from one year's increment to the next. It is thus seen that in the distribution of its sporangia *Isoetes* shows a condition similar to that of *Lycopodium Selago*, but that the various degrees of their abortion are better represented. It is, however, with the dendroid Lycopodiales that *Isoetes* shows common characters of the sporangia themselves ; there is also some similarity to them in the structure of its abbreviated but bulky stock : on this also the very similar bifurcating roots are inserted, but in *Isoetes* their origin is localised in the depressed grooves which traverse the stock longitudinally, instead of their being borne on Stigmarian outgrowths, as in the fossils. The *Isoetes* plant is then like a partially differentiated strobilus seated upon a Stigmarian base ; in fact, like a stunted *Lepidodendron* or *Sigillaria* with its preliminary vegetative phase very short. In order to aid these comparisons Hirmer's reconstruction of a *Lepidodendron* plant may be inserted here as Fig. 165.

The account thus given of the general morphology of the mature sporophyte in the Lycopodiales, living and fossil, shows the essential identity of their plan of construction throughout the phylum, and how in the two series, the ligulate and the eligulate, parallel conditions of differentiation are represented. In both the structure of the shoot is essentially strobiloid, with a very constant numerical relation of the sporangium in the fertile shoot to the subtending sporophyll. In both series the branching of the axis is primarily by dichotomy, with a deviation in the more specialised types, and particularly in the higher ramifications, to the monopodial branching ; but in certain simple types branching is rare, or even absent. The shoot is fixed in the soil by roots, formed chiefly, or even exclusively, at the base of the axis in the simpler types ; but in the more specialised they may be formed at various other points on the shoot-system, or on outgrowths from it of an indeterminate character. In both series there is evidence of abortion of sporangia, leading to a segregation of definite tracts of the shoot-system devoted respectively to nutrition and to propagation : in the higher types the strobilus becomes a definite cone of limited growth, clearly marked off from the lower vegetative region ; the production of spores is thus deferred in the individual life, and a more lengthy vegetative phase intervenes before that event. This progressive differentiation is best illustrated in the eligulate series, which is also the more primitive in respect of its homosporous condition.

CHAPTER XII

ANATOMY OF THE LYCOPODIALES

It has been seen that in the Lycopodiales the leaves are relatively small, while the axis is the dominant feature of the shoot. Also, that in many of

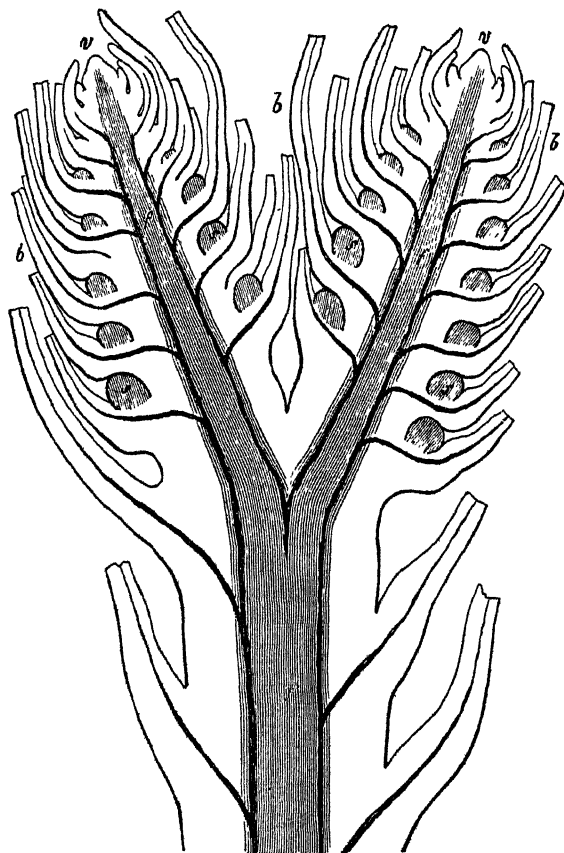


FIG. 166.

A forked sporangiferous branch of *Lycopodium chamaecyparissus* in longitudinal section, slightly magnified. *ff*=the axile vascular body. *bb*=leaves. *ss*=young sporangia. (After Sachs.)

them the sterile and fertile regions are not strongly differentiated, the axis being continuous from the one to the other. It may then be anticipated that

the structure of the axis of the cone will resemble that of the sterile stem, of which it is a direct continuation (Fig. 166). In both the stem is traversed by a massive monostele with peripheral protoxylem, and upon this the relatively thin leaf-traces are inserted with a minimum of local disturbance. The simple vascular system so constructed is embedded in a broad cortex, which often shows considerable differentiation in structure, while superficially there is an epidermis which is frequently thick-walled. A comparative examination of the various forms of Lycopods shows that the non-medullated monostele may be accepted as a central type for them all, upon which certain modifications and variants have arisen in accordance with habit and increasing size.

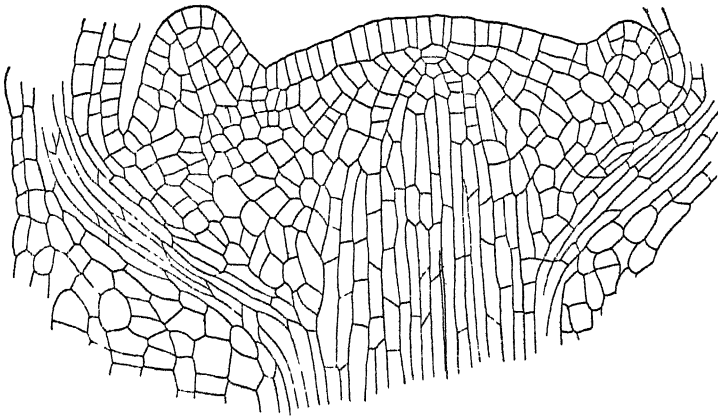


FIG. 167.
Longitudinal section through the apical cone of the stem of *Lycopodium Selago*. $\times 160$.
(After Strasburger.)

The vascular skeleton of an adult shoot is shown in longitudinal section in Fig. 166. The stele may be followed upwards to the growing apex, and it terminates at a point closely below the group of initial cells (Fig. 167). In the adult stem these are prismatic in form, and three in number—only two being visible in the longitudinal section. By growth and segmentation these cells give rise to the whole of the shoot. If the apical region be examined the plerome-cylinder is seen to extend beyond the youngest leaves, to a point immediately below the apical group of cells; thus the central region at least of the adult stele is *cauline* in its origin. The leaves originate from the three or four outer layers of cells of the growing point, quite apart from the plerome, while their procambium strands become differentiated in the intervening tissue, finally forming connection with the central cylinder; upon this they are inserted laterally, the protoxylem-groups connecting with the projecting flanges of wood. Thus in the ontogeny of the microphyllous shoot the leaf is an accessory which arises after the stele is already in existence. Its relative unimportance is not only apparent from this late origin, but also from

the fact that the arrangement of the leaves upon the shoot does not dominate the number or position of the protoxylem-groups of the stele. Particularly is this so where the numbers are large : for instance, in *L. clavatum* Jones¹ has found that though in shoots with a simple leaf-arrangement it is usual

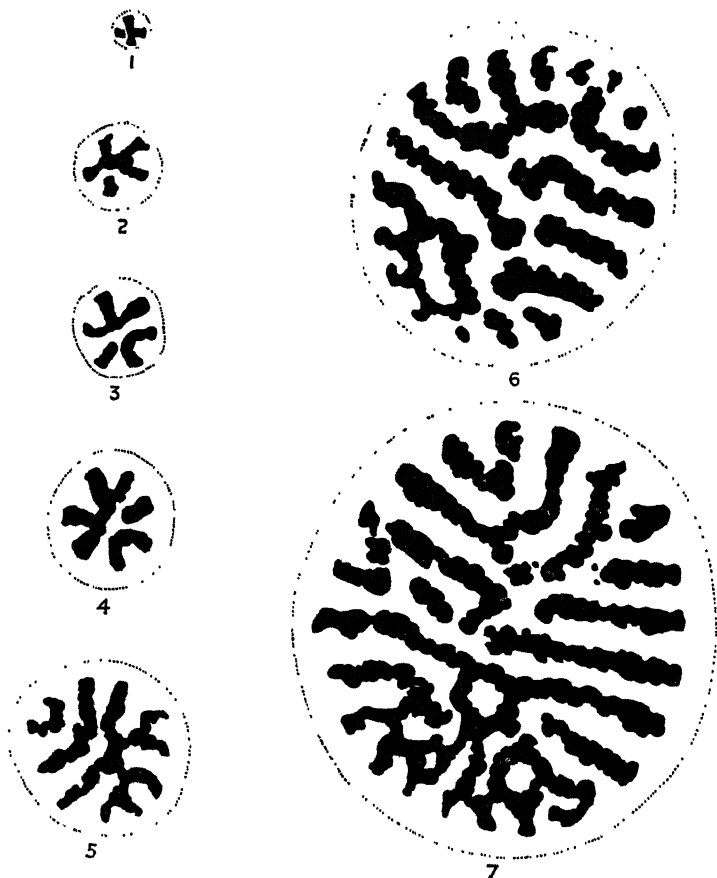


FIG. 168.

Lycopodium scariosum, var. *Jussiaei*, Desv. 1, stele of a sporeling, after Holloway; 2, section from a fine distal twig; 3-7, sections from branches successively of greater thickness. Xylem black; limit of stele dotted. All magnified 50. (After Wardlaw.)

for the protoxylems to correspond to the leaf-insertions, where the number of flanges is more than six no such correspondence is maintained. Such facts indicate that in the adult state of *Lycopodium* the axis is the dominant feature of the microphyllous shoot. This conclusion may be held to apply for the Lycopods at large.

The living genus *Lycopodium* has elaborated the non-medullated mono-stele along relatively conservative lines, and the results of this will be described

¹ *Trans. Linn. Soc.*, vol. vii., 1905, p. 19.

first. The sporeling of *Lycopodium*, like that of other Pteridophytes, starts away with a small solid core of dead tracheides surrounded by living tissue. As the stem enlarges conically upwards this core becomes grooved by intrusion of softer tissues, a protoxylem-group occupying the margin of each projecting flange. The number of the grooves increases with the size of the stele (Fig. 168, 1); moreover, by further encroachment of the living tissue upon the stellate tract of dead wood this becomes disintegrated as seen in transverse section (2-4). These changes continue with further increase in size until the number of apparently separate tracts of wood is very large (6-7). But longitudinal sections show that those tracts are not distinct from one another for any great distance up or down; the real structure of the wood is that of a xylem-sponge, which has the effect of serving as a continuous means of water transport, and at the same time of tending to maintain a due proportion of surface of living tissue adjoining the dead tracheides,

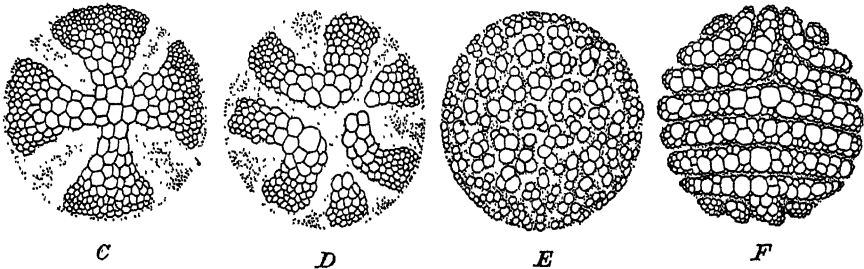


FIG. 169.

Diagrammatic transverse sections of the stele of various species of *Lycopodium*; the phloem is dotted, the xylem drawn as tracheides. C=*Lyc. serratum*, Thbg., with stellate arrangement. D=upright stem of *L. annotinum*, L., with somewhat stellate arrangement. E=*L. cernuum*, L., with uniform distribution of the small groups. F=*L. volatile*, Forst., with strongly bilateral structure. $\times 80$. (From Engler and Prantl.)

as the size increases. In the adult stems of various species there is considerable difference in detail of this xylem-sponge, and its structure is related to habit. Thus in the section *Selago*, as seen in *L. Selago*, *serratum*, and *lucidulum*, the stele is found to consist of a connected central mass of xylem of irregularly star-like form; the rays of the star vary in number in different species, as well as in different regions of the same plant, and are specially characterised by the form of the periphery of the rays: these may expand outwards into a wide-spread, almost fan-like outline, as seen in the transverse section (Fig. 169, C). Small tracheides forming the protoxylem lie at the extreme periphery, while the centrally-disposed metaxylem is composed of larger elements without any parenchyma interspersed between them. The spaces between the xylem-rays are occupied by the sieve-tubes, with the protophloem lying at the periphery, while conjunctive parenchyma forms a complete sheath intervening between the phloem and the xylem. The whole is invested by a parenchymatous sheath resembling a pericycle, but derived from the cortex; outside this is an endodermis, recognisable while

young as a single layer, but later obscured by extension of the corky development. A similar structure to the above is seen also in the thinner branches of *L. inundatum*, a species which stands in its external morphology in near relation to the section *Selago*. These species may be taken as representing the structure usually found in the simpler upright, ground-growing members of the genus.

But a more elaborate construction of the stele is found to accompany a greater differentiation of external form. In creeping and climbing stems there is apt to be a development of alternating bands of xylem and phloem: the xylem becomes isolated into distinct plates as seen in the transverse section, and these are roughly disposed parallel to the surface of the substratum (Fig. 169, *F*). In other cases the xylem and phloem are more uniformly distributed, the former as patches embedded in the latter, as seen in transverse section (Fig. 169, *E*). Both these conditions may be connected by intermediate steps with the simpler type seen in *L. Selago*. In point of fact these all appear more different as seen in transverse section than they are in reality. All of them spring from a common source. By comparison within the genus it may be figured how from the condition of a primitive protostele, with phloem about its periphery, the modern Lycopod-stele became in the more advanced cases a variously moulded xylem-sponge, with phloem and conjunctive parenchyma occupying the interstices. On the other hand, it will be seen later that the simple cylindrical protostele, enlarged but without intrusive phloem, is habitual among the fossil Lycopods; but they are all extinct. It is possible that the elaboration seen in the steles of the living genus as the size increases may have been one of the conditions of survival.

In *Phylloglossum*, the stelar structure is often rudimentary. It there consists of a lax association of leaf-traces, each with mesarch structure. But in the largest specimens of the peduncle, such as that shown by Bertrand in his Fig. 95 (*Arch. Bot. du Nord de la France*, p. 106), the appearance is as of a medullated monostele with a continuous xylem-ring, upon which the monarch leaf-traces are inserted peripherally. This suggests a comparison with small distal shoots of *Lepidodendron* rather than with the modern *Lycopodium*. Hitherto little definite knowledge of the anatomy of the smaller eligulate fossils included under the name of *Lycopodites* has come to hand. Whenever such facts are available they will provide interesting material for comparison with the modern species of *Lycopodium*.

Turning to the Ligulate Lycopodiales, the living species of *Selaginella* afford material of particular interest in its bearing on stelar morphology. It has been concluded that the radial type is relatively primitive, and the anatomy of *S. spinulosa* will be taken first. The thin trailing stem contains a protostele with protoxylem in the centre of a cylindrical strand (Fig. 170, *A*): externally lie phloem and pericycle, and the whole is suspended in an air-cavity by the well-known trabecular endodermis of the genus. In its course

upwards the protoxylem divides and passes to the periphery of the woody tract (*C-F*), its several strands being seated on slightly projecting flanges (*G, H*). On entering the cone the woody tract expands and becomes medullated, thin-walled cells replacing the innermost tracheides; towards the tip of the cone the woody leaf-trace-strands become isolated after the manner of *Tmesipteris* (Fig. 91) or *Lepidostrobus Brownii* (Fig. 175). Though on a

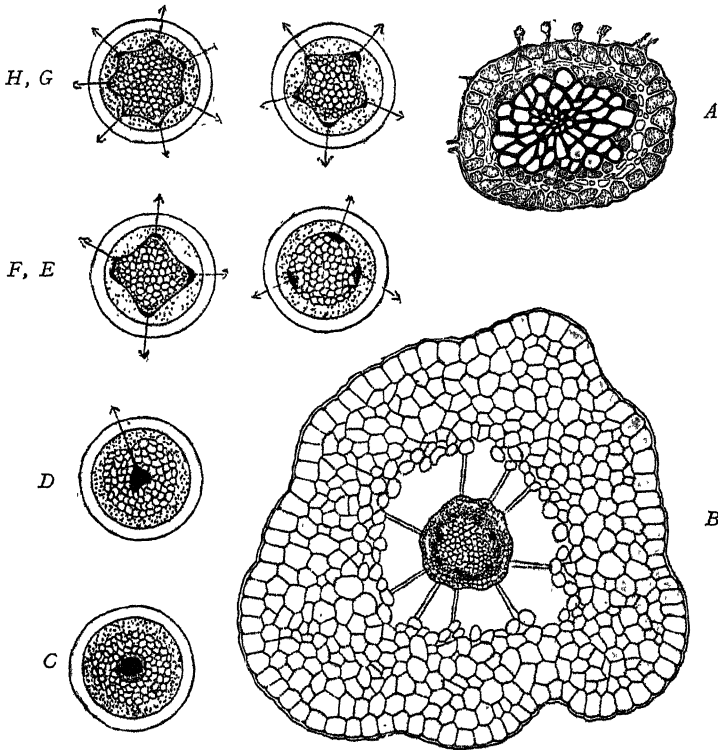


FIG. 170.

Selaginella spinulosa. A. Transverse section of the stele of a trailing stem showing central protoxylem. a=pericycle; b=protophloem; c=phloem parenchyma; d=metaxylem. $\times 275$. B=transverse section of upper part of axis, showing a stele with seven protoxylems; the trabecular endodermis is well shown. $\times 350$. C-H=scheme of arrangement of the protoxylems in sections taken successively from below upwards. (After Harvey-Gibson.)

very small scale this vascular system is comparable with that of *Lepidodendron*, particularly in its originally solid and ultimately medullated woody core, with its external fluting and its final separation of the tracheidal traces.

The dorsiventral Selaginellas take a different course. The stele has the form of a flattened ribbon, and the purely tracheidal wood the same, with its protoxylems at the two margins. The larger the stem the wider is the ribbon, as shown by comparing *S. Martensii* with *S. grandis* (Wardlaw, *Trans. R.S.*

Edin., vol. liv., p. 283, Fig. 1; or Bower, *Size and Form*, Fig. 8). But where the size is great, as in the climbing stem of *S. Willdenovii* and some others, a more complicated disposition of the conducting tracts is seen; the steps of complexity following on the increasing size upwards are shown in Fig. 171, in sections taken successively from the same stem. The shoot sprang from a creeping rhizome. At the base it was monostelic with a ribbon-shaped xylem (1); on passing upwards the stele increased in girth, and changes appeared which were at first intra-stelar (2-4), leading to the separation of three distinct stelar bands (5). With further increase in size elaborations of

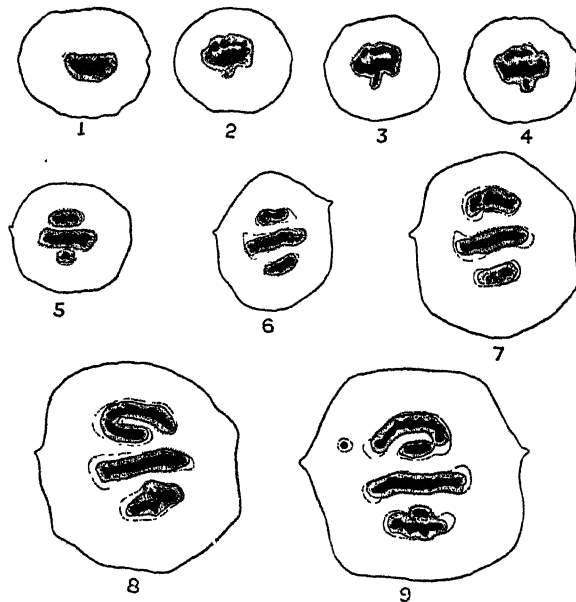


FIG. 171.

Selaginella Willdenovii. Sections of the aerial stem: 1, from base of shoot, near junction with the creeping stem; 2-5, transitions to the tristelic state, showing the method of formation of the dorsal and ventral steles; 6-9, sections successively higher in the same shoot, showing origin of additional stelar ribbons. All $\times 9$. (After Wardlaw.)

the dorsal and ventral meristeles point towards further segregation, and may result in small additional meristeles, making five in all (8, 9). Meanwhile leaf-traces are given off: most of these arise from the margins of the median meristele, but some of them spring from the others as well. These structural facts represent an adjustment of form of the conducting tracts as they increase in size within the firm sclerotic rind. They tend to maintain a due proportion of presentation-surface of the dead tracheidal tract to the living tissue that surrounds it. The solution of the problem is essentially like that seen in *Lycopodium* (Fig. 168), but carried out in terms of the structure characteristic of *Selaginella*, with complete polystelic results.

A third type of stelar adjustment is seen in *S. laevigata*, var. *I. yallii*, and in a minor degree also in *S. uliginosa*. In the young rhizome the stele first

becomes solenoxyletic (Fig. 172, 1), but later solenostelic (2), and with further enlargement polycyclic, after the manner of certain Ferns (3, 4) (compare Bruchmann, *Flora*, vol. 99, p. 436). But this is not all, for in the upright



FIG. 172.

Steles from the rhizome of *Selaginella Lyallii*, uniformly magnified; xylem black, phloem and parenchyma stippled; the dotted line is endodermis. 1, solenoxyletic stele of thin rhizome; 2-4, ascending series of sections of the same rhizome, showing progressive complexity with increasing size. All $\times 23$. (After Wardlaw.)

stems of the same species the solenostele is seen to break up into many meristeles, thus attaining the dialystelic state seen in many Ferns (Fig. 173, 1-6). Wardlaw has shown experimentally that when the upright axis, having this

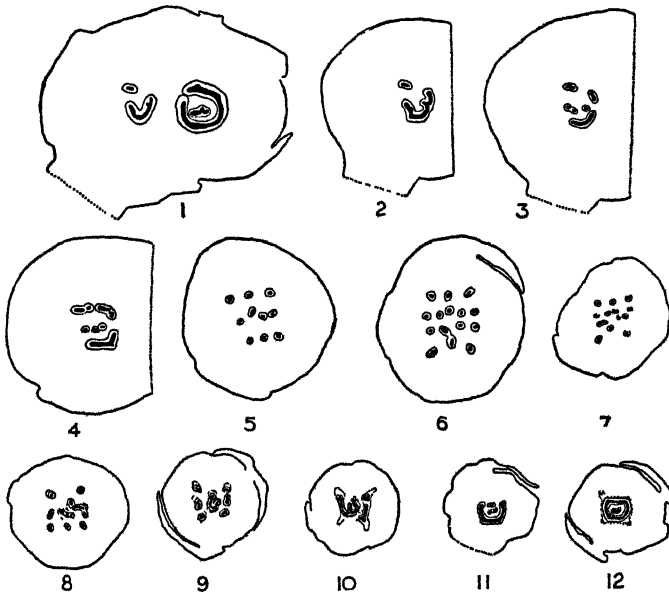


FIG. 173.

Selaginella Lyallii. Successive sections from the stem, drawn to the same scale. 1-6, show the transition from solenostely to dialystely at the base of the erect axis; 7-12 were taken from an erect axis laid horizontally so as to resume in its further growth the character of a rhizome. The reversion to solenostely has followed. (After Wardlaw.)

structure, is laid horizontally and induced to grow as a typical rhizome, the solenostelic state is resumed by fusion of the meristeles (Fig. 173, 7-12).¹ It seems highly improbable that there is any near phyletic relation that would

¹ For a further discussion of these remarkable facts see Bower, *Size and Form*, pp. 31-38.

explain the structural parallel between these Selaginellas and relatively advanced Ferns. A more probable view would be that they represent homoplastic responses to like conditions.

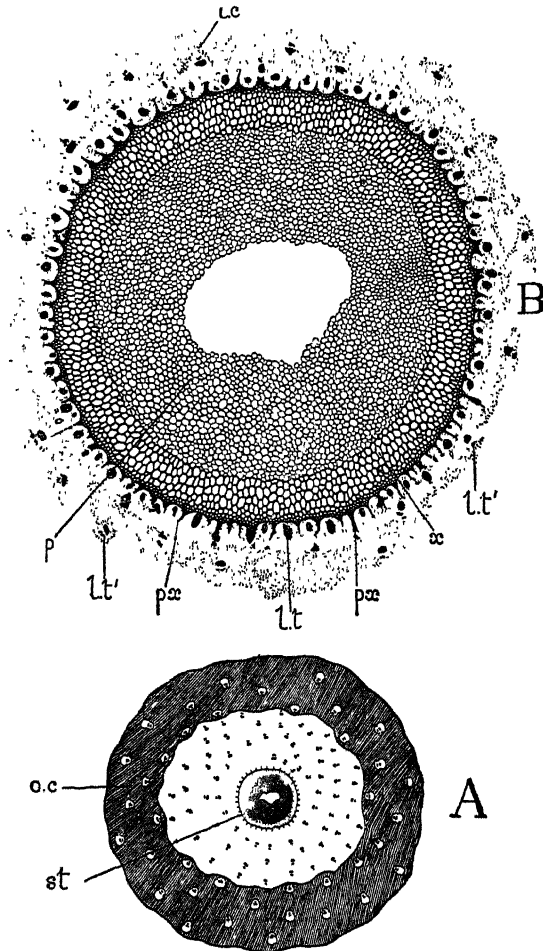


FIG. 174.

Lepidodendron Harcourtii. A=transverse section of stem; st=stele; o.c.=outer cortex; both here and in the outer cortex the leaf-traces are shown about natural size. B=stele of same; p=pith, hollow in the middle; x=xylem-ring; px=protoxylem-points. The leaf-traces join the stele between them; lt=leaf-trace bundles, of which the outer, lt', show xylem and phloem; i.c.=inner cortex. $\times 7$. (From Scott's *Studies in Fossil Botany*.)

The near correspondence of the ancient *Lepidodendron*-type to that of the modern Lycopodiales appears not only in their external form, but also in their internal structure, though special modifications of type, different from those of the modern forms, appear in accordance with the larger dimensions so prevalent in the fossils. The similarity consists in the presence of a single

columnar stele, with centripetal wood and peripheral protoxylem, in relation to which the leaf-traces are inserted with the minimum of local disturbance.

The general structure of one of the more simple types may be gathered from Scott's figure of *Lepidodendron Harcourtii* (Fig. 174), which shows (*A*) the relatively small proportion of the stele to the whole axis; (*B*) the peripheral protoxylem, with its relation to the incoming leaf-traces, and the uninterrupted ring of metaxylem, not separated into strands; while centrally

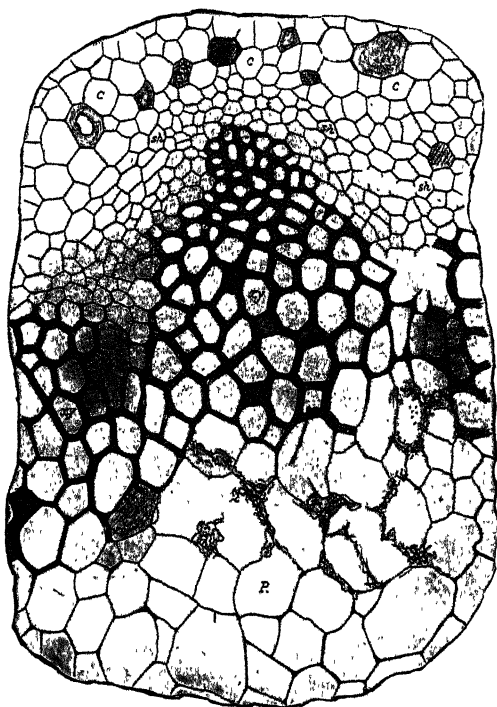


FIG. 175.

Lepidostrobus Brownii. Part of a transverse section showing the central parenchymatous pith (*p*), the wood (*w*), the innermost band of cortex (*c*). $\times 200$.

a large pith is seen hollow in the middle. The steles of *Lepidodendron* varied in structure towards the centre: in some cases, such as the very ancient *Lepidodendron rhodumnense*, Renault, and *Lepidodendron saalfeldense*, Solms, from the Culm, there was a solid stele, without secondary thickening; or, as in *Lepidodendron Petticurensis*, Kidston (*Roy. Soc. Edin. Proc.*, 1906-7, p. 207), the solid xylem-core was surrounded by secondary wood. But often, and especially in more recent forms, the xylem was medullated, and in this they differ from modern Lycopods. It is obvious in some cases that the pith originated by incomplete development of tissue originally tracheidal: this is clearly indicated in Fig. 175. This drawing also shows

that outside the xylem came a narrow band, probably of phloem, which is usually ill preserved. Thus, putting aside the larger size, and the medullation which is its frequent concomitant, there is substantial similarity in the structure of the stele to that of a simple *Lycopodium*, or of *Selaginella spinulosa* at its distal region.

The phloem of the Lepidodendroid stems is usually ill-preserved, and the descriptions have been meagre. But latterly examples have been obtained which show it as a well-developed band. It is hardly represented at all in the distal end of the cone of *Lepidostrobus Brownii* (Fig. 175); but it has lately been demonstrated in a vegetative stem ascribed to this plant. There it appears as consisting of large lax tubes abutting outwards on the inner cortex, and separated inwards from the wood by 2-3 rows of parenchyma (Calder, *Trans. R.S. Edin.*, 1933, p. 549). In a stem of *Lepidophloios* from East Kilbride, soon to be described by Walton, there is an interrupted band of phloem outside the solid core of wood. Leaf-traces pass out at the gaps, the wood carrying out with it a tract of phloem, and thus showing a collateral structure of the trace. Here again the phloem consists of large lax tubes, as seen in transverse section.

Fluting of the outer surface of the primary tracheidal column is a frequent feature in the fossil Lycopods. The result is to form a "corona" of concave crenulations, as seen in *L. Harcourtii* (Fig. 174). The first impulse may be to assume that the projecting teeth represent the insertions of leaf-traces: this may sometimes be true, but it is not uniform. For instance, in *L. Harcourtii* and generally in *Sigillaria* they are given off from the concavities between the projecting teeth. Thus crenulation appears to be a feature independent of leaf-insertion, and the fluting is a feature of the stele itself. This is in accord with what has been seen as to the insertion of the leaf-traces in *Lycopodium* and in *Selaginella*. In none of these does the leaf-trace-insertion bear a constant relation to the detailed contour of the wood.

A more striking concomitant of the larger growth appears as the *secondary thickening* represented in the majority of the known species of *Lepidodendron*, though absent from some of the earliest. It was carried out by two distinct zones of cambial activity, the one immediately surrounding the primary xylem, and resulting in a band of radially seriated secondary wood, contiguous usually with the protoxylem of the primary development. Externally an exiguous secondary phloem appears (Fig. 176). Outside the thickening ring of the stele a second zone of cambial activity arises in the cortex, below the persistent bases of the leaves: this results in the formation of a broad band of secondary cortical tissue, or periderm. Such cambial activity extended from the main trunk into the branches, and in some cases into those of quite moderate dimensions. Comparison of the various known types of *Lepidodendron* suggest unmistakably that even the most elaborate are the result of expansion of a non-medullated monostelic construction, to serve dendroid purposes. A first step, following on the increasing size of the stele,

would usually be the formation of a parenchymatous pith; this appears to have originated directly, by the incomplete development of a primitively solid tracheidal core, as is suggested in the case of *L. Brownii*; and in support of this it is found that tracheides and parenchymatous cells may be intermixed in the central region, a condition held to represent an imperfectly

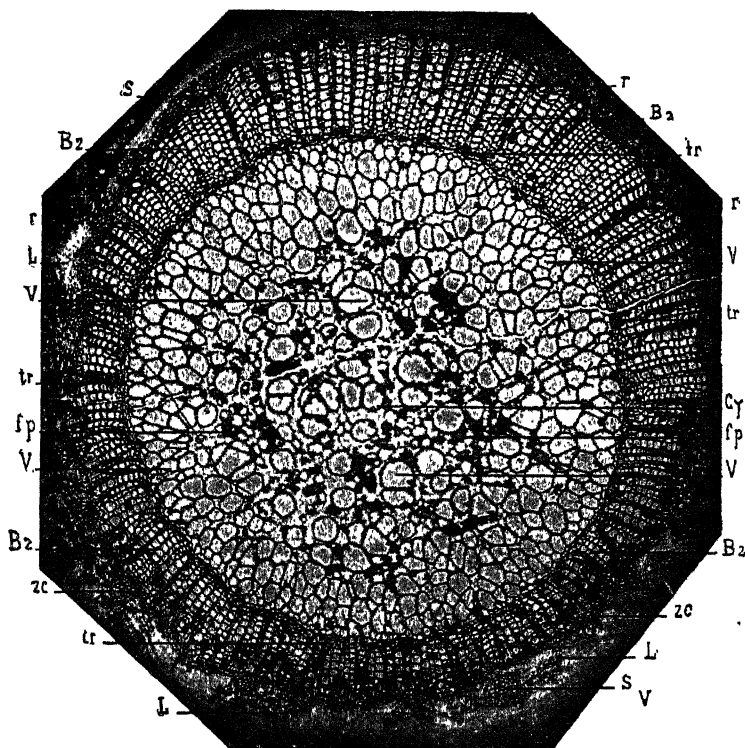


FIG. 176.

Transverse section of an axis of *Lepidodendron selaginoides*. Cy=centre of the vascular system; tr=tracheae; V=vessels of the primary cylinder; fp=primitive fibres of the primary wood; B₂=tracheides of the secondary wood; r=ray of the secondary wood; p₂=secondary parenchyma; zc=cambial zone; L=liber; s=foliar traces detached from the primary cylinder. (After Hovelacque.)

formed pith: it is seen in *L. selaginoides* (Fig. 176). It would seem probable that the non-medullated condition, so persistently maintained in the smaller living Lycopods, was the primitive state also for the larger dendroid fossils. The other factor of expansion, by cambial activity, appears to have originated independently of medullation, since it occurs both in medullated and in non-medullated axes.

However large the proportion of pith to the primary wood became in *Lepidodendron*, the continuity of the ring was as a rule unbroken, and the leaf-traces were simply inserted upon the primary xylem with the minimum

of local disturbance. But in *Sigillaria*, in which the leaves sometimes attained a very large size, the case is different: though they show in all essentials the same construction of the stele as in *Lepidodendron*, they illustrate steps towards the breaking up of the primary wood of the medullated stele into separate strands. The details derived from various Sigillarian fossils have been put together in stratigraphical sequence by Kidston (*Trans. R.S. Edin.*, vol. xvi., part iii., No. 23). He has shown that the condition with primary xylem forming a closed ring surrounding a large medulla was the most primitive for *Sigillaria*: such structure is found in the more ancient

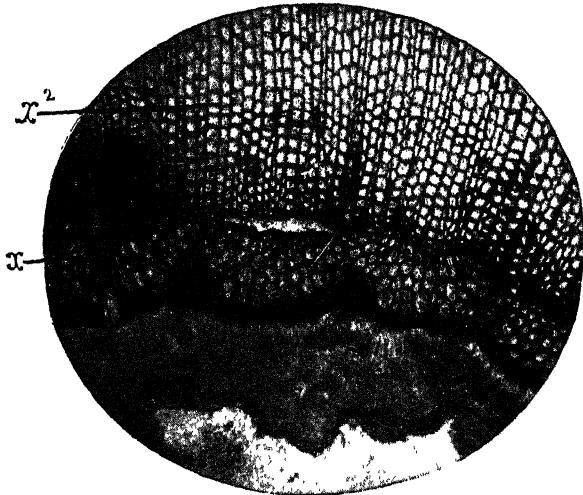


FIG. 177.

Sigillaria spinulosa. Part of the wood, highly magnified, showing separate primary strands (x) and secondary wood (x²). $\times 18$. (After Scott, from photographs by Dr. R. Kidston.)

specimens from the Lower Coal Measures (*S. elongata*, Brongn., and *S. elegans*, Brongn.); those from the lower Permian, however (*S. menardi*, Brongn., and *S. spinulosa*, Rost. sp.), show the primary xylem as a circle of separate bundles, though some of them may cohere laterally in the last-named species (Fig. 177). In such forms, the pith being of relatively very large size, the primary wood is reduced to a comparatively narrow investment round it, liable, as we have seen, to be broken up into distinct strands. Secondary tissues make their appearance, however, as in *Lepidodendron*, there being in *Sigillaria* a broad zone of secondary xylem, and a highly organised periderm. It is thus seen that the later *Sigillarias* have departed further in their structure from the simple protostele than other dendroid Lycopods, for in them not only is there medullation, and a secondary thickening, but breaking up of the primary xylem as well.

Passing in conclusion to the living genus *Isoetes*, it has been seen from external comparison that the whole plant is like a partially differentiated

Lepidostrobus seated upon a Stigmarian base. The question will now be how far its anatomy will countenance this view. Von Mohl as early as 1840 gave a wonderfully clear account of the morphology and anatomy of the stock of *Isoetes* (Von Mohl, *Verm. Schriften*, p. 122). From his sections of it taken in three planes the fact emerges vividly that the central vascular system of *Isoetes* can be distinguished into an upper cylindrical stem-stele giving off the leaf-traces; and a lower region of the stele extended in the plane of the groove. From this lower region, and in acropetal relation to its downwardly directed edge, the root-traces arise. It is noteworthy that Von Mohl was interested in the question as to whether *Isoetes*, unlike other vascular Cryptogams, had something corresponding to a "*caudex descendens*," or tap-root. Williamson, approaching the question from the side of the morphology of the dendroid Lycopodiales, makes the clear comparison of the lower, root-bearing region of *Isoetes* not with a tap-root, but with the Stigmarian system of a *Lepidodendron*. As a modern version of the position of Von Mohl and of Williamson, reference may be made to Lang.¹ From his description it appears that the primary vascular structure of the stock is in accord with the interpretation derived as above from external comparison.

The secondary thickening of *Isoetes* is anomalous, and this has led to some misunderstanding. The cambial layer is established not between the primary xylem and phloem, but outside the primary phloem of the stele (see Lang, 1915, part ii., p. 29). It produces internally a secondary tissue with its elements arranged in radial rows. From its appearance this has been distinguished as prismatic tissue. Its elements may be developed as tracheides, sieve-tubes, or as parenchyma. This secondary thickening is comparable with that of *Lepidodendron*, and especially with the anomalous thickening found in such forms as *L. fuliginosus*.² Following this interpretation the anatomical structure accords with the morphological view based upon external features.

LEAVES

The adult leaves of *Lycopodium* and *Selaginella* are small compared with those of most of the fossils. In *Lycopodium clavatum* the blade is triangular in transverse section, and is traversed by a single small vascular strand surrounded by spongy mesophyll, and by epidermis which bears stomata on both surfaces. In the leaf of *Selaginella Martensii* the flattened blade also has a single vascular strand, surrounded by spongy parenchyma which fades out towards the margins. The upper epidermis consists of conical cells with very large chloroplasts, and there are no stomata; the cells of the

¹ *Proc. Manch. Lit. and Phil. Soc.*, vol. 59, 1915; part i, p. 1; part ii., p. 29. Here full quotation of the literature is given.

² See Scott's *Studies*, 3rd edn., vol. i., p. 137; vol. ii., p. 401; also Seward, *Fossil Plants*, ii., pp. 147, 148.

The roots are seen to arise in *Lycopodium* directly from the axis, sometimes in upright species taking an internal course to the base of the stem through the soft middle cortex (*L. Selago*). In *Selaginella* they spring from the basal knot in radial types (Fig. 149): or in others from the rhizophores. In the Lycopodioid fossils they arise from the Stigmarian trunks, and in *Isoetes* from the lower portion of the short stock. The conclusion has already been drawn that the rhizophores of *Selaginella* are best ranked as parts of indeterminate character, and the same appears to hold for the Stigmarian Trunks. The external appearance of these has already been described: their anatomical structure, and particularly their relation to the true rootlets, offers features of interest. A well-developed vascular cylinder lies centrally surrounded by cortex and periderm. The outer and inner

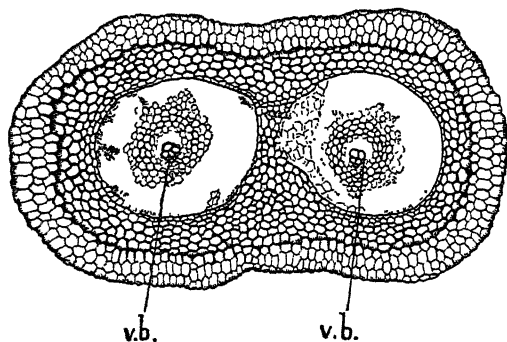


FIG. 180.

Stigmaria ficoides. Transverse section of rootlet, showing dichotomy. The outer cortex, differentiated into two zones, is still continuous, while the inner cortex of the two branches has completely divided. v.b., the two monarch vascular bundles. $\times 25$. (After Scott.)

cortex are resistant, and are usually well preserved; but the soft middle cortex is often absent. The stele consists of a central core, which appears occasionally as a solid mass of centripetal tracheides, as in *Stigmaria Lohesti* from the English Coal Measures (Weiss, *Manch. Lit. and Phil.*, 1929); but usually the centre is occupied by pith, and centripetal wood may be absent. It seems probable that the former is the more primitive type of structure. The primary wood is surrounded by a broad zone of secondary xylem divided up into bundles by the principal medullary rays. Externally remains of a cambium may be traced, and a delicate outer tissue, presumably phloem. As a whole this structure corresponds in essentials with that of certain types of *Lepidodendron* stem. From it the rootlets radiate outwards, being inserted with regular quincuncial arrangement. For further details reference must be made to works on Fossil Botany.

The structural comparison of the rootlets with the roots of *Isoetes* naturally involves the morphological interpretation of the stock upon which those rootlets are respectively borne. A view which appears most probable,

and at the same time consistent with the anatomical findings, is that in all of these Lycopods the roots are liable to be borne upon organs of indeterminate character: neither, strictly speaking, stems or roots. Of these the most problematical are the root-bearing clefts of the stock of *Isoetes*. The key to these is probably to be found in *Pleuromeia*, with its abbreviated Stigmarian Trunks. These if involuted and their surfaces concave instead of convex, like a glove finger turned inside out, would give the same orientation of the protoxylem of the rootlets as in *Isoetes*, that is towards the base of the indentation, as they actually present to the Stigmarian apex. In this interpretation the lines of indentation of the *Isoetes* stock would not correspond to the crossed lines of demarcation of the four Stigmarian Trunks, as seen on an upturned base of *Lepidodendron*. They would correspond rather to the flattened conical tips of the Stigmarian Trunks.

Anatomical comparison of the various types of Lycopods in the adult state, and particularly of their conducting tracts, has shown that they may all be traced in origin to a simple protostelic type, having a solid tracheidal core with external coverings of phloem and cortex. This is suggested by the ontogeny of the living types, while the final structure whether of these or of the fossils may be held as illustrating their divergent development, in the solution of problems presented by increasing size. In this, as is natural in microphyllous types, the leaf-trace is a minor factor, and it is the axis which is dominant throughout, though less markedly in *Isoetes* where the leaf is relatively large. *Lycopodium* and *Selaginella* have built their adult vascular structure upon the basis of primary xylem, which is purely tracheidal. They have met the demands for maintenance of presentation-surface, as the size increases, by elaboration of the form of the woody tracts, or even of the stele itself. Some *Selaginellas* have even adopted mouldings of the stele parallel to those seen in advanced Ferns. In the fossils the elaborations in relation to increasing size are for the most part based upon medullation usually combined with cambial thickening. The results find their parallel in many other land-plants of dendroid type; but among the living Lycopods the cambial thickening appears in a highly specialised and anomalous form in the stock of *Isoetes*. There is hardly any Class of Plants in which such variety of resource in meeting the demands of increasing size is to be found. But the remarkable fact is that the fossil types are more advanced in certain of their methods than are the living Lycopods. Perhaps the uniformly small size of these may be correlated with the persistence with which *Lycopodium* and *Selaginella* have neglected the use of cambium as a solution of the difficulties inherent in increasing size, and have based their adult structure solely upon the primary tissues.

CHAPTER XIII

SPORE-PRODUCING MEMBERS OF THE LYCOPODIALES

THE sporangia typical of the Lycopodiales are non-septate sacs. The form is that of a kidney, of which the curvature and proportions are liable to considerable variation (Figs. 149-152). The position is essentially constant, each sporangium being inserted in a median position relatively to its subtending sporophyll. The curvature is in a tangential plane, showing a more or less pronounced fan-like outline. A series of examples of sporangia will be selected as illustrating the structure and mode of development, and the degree

of variation in form and proportion which exists within the Class.

The genus *Lycopodium* will be taken first, and the sporangia compared in a number of species. It will become apparent from this comparison that the differences which they show are not at haphazard, but that they follow with some degree of accuracy those lines of external differentiation, upon which the systematic arrangement of the genus has been based. In order to make this clear the description will follow the accepted systematic order, beginning with the least differentiated types. In *L. Selago* the sporangium originates at the base of the sporophyll, but definitely upon

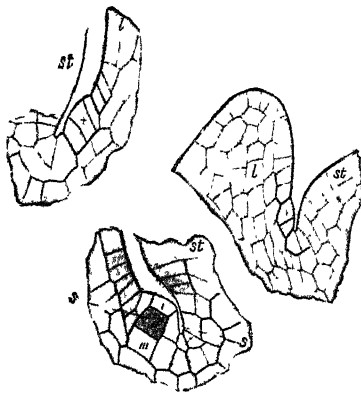


FIG. 181.

Radial sections through young sporangia of *Lycopodium Selago*. In the youngest the whole sporophyll is shown (*l*), and the axis (*st*), and it is seen that the sporangium arises upon the surface of the sporophyll. The older stages show the segmentation of the sporangium. $\times 200$.

its upper surface as a tangentially extended cushion (Fig. 182, *A*). In median radial section it appears as a convex growth, in which a central row of three cells, the result of periclinal division of one parent cell, is dominant (Fig. 181, *i*, *ii*, *iii*): of these the middle cell (*ii*) is of archesporial character. A tangential section of a sporangium of similar age (Fig. 182, *B*) shows that there are a number of these archesporial cells: in the example shown there are seven; but the number is not constant, as is seen by comparison of various tangential sections, and supported by sections cut transversely (Fig. 182, *C*). The young sporangium consists thus of a single tangential

row of archesporial cells, covered in completely by a single layer of cells forming the sporangial wall, and supported below, by cells which grow more actively in the middle region of the sporangium, thus leading to the curved form which it assumes later. At first the parts thus laid down grow uniformly; but the later divisions are less regular. Superficially they result in the formation of a sporangial wall, composed of three layers, or of more towards the base of the sporangium (Fig. 182, *D*): of these the innermost is the transitory tapetum; the tapetal investment of the sporogenous tissue is completed by development of the adjacent cells of the sub-archesporial

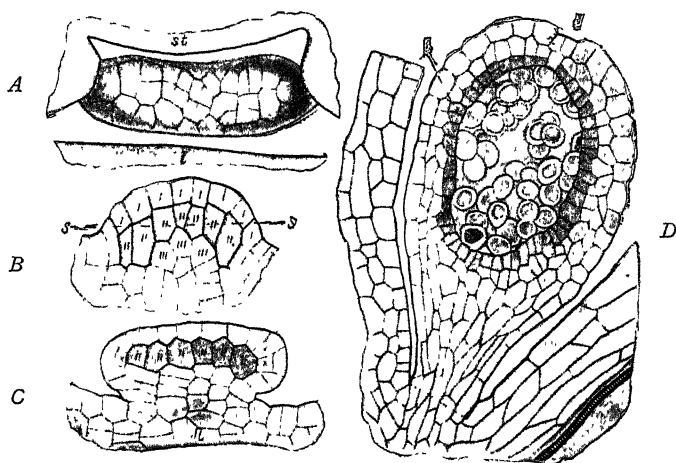


FIG. 182.

Lycopodium Selago. *A*=young sporangium seen in superficial view: *st*=stem; *l*=sporophyll. *B*=tangential section of a similar sporangium; the cells numbered *i*, *ii*, *iii* correspond to those similarly marked in Fig. 181. *C*=a sporangium of like age in transverse section, as along a line *s, s*, in Fig. *B*. The archesporial cells are shaded. *D*=an older sporangium, in radial section, showing the spore-mother-cells separated, before tetrad-division. *A*, *B*, *C* $\times 200$. *D* $\times 100$.

tissue also as tapetum. The dehiscence is along a tangential line, and the preparation for this is already indicated at the distal end in Fig. 182, *D*, *d*. Meanwhile, the sporogenous group within has been subject to repeated cell division: its cells finally separate, round themselves off, and all of them, as a rule, undergo the tetrad-division. In the mature sporangium the form is less strongly curved in *L. Selago* than in many other species, while the stalk is a relatively narrow one. The general proportions, as well as the imperfect protection of the sporangium afforded by the rather narrow sporophylls, are shown in Fig. 183, *d*, *e*, *f*. The subtending leaf resembles the foliage leaf, being photosynthetic, and it often bears a basal mucilage cavity (Sykes, *New Phyt.*, vii., p. 41).

The type of sporangium thus described for *L. Selago* appears to be characteristic, with relatively slight modifications, of the sub-genus *Urostachya*: other species of the sub-genus which have been examined, viz., *L. dich-*

tomum, Jacq., *carinatum*, Desv., *nummularifolium*, Blume, and *Phlegmaria*, L., are all alike in showing an archesporium consisting of a single tangential

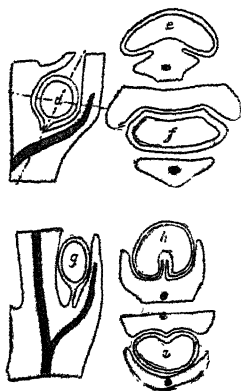


FIG. 183.
d, e, f=sections radial, tangential, and transverse of mature sporangia of *Lycopodium Selago*. g, h, i= similar sections of mature sporangia of *Lycopodium phlegmaria*. $\times 12$.

row of cells, though the number of these in the row may vary. The further development in these species was also the same as in *L. Selago*, though the proportions were different. In *L. dichotomum*, however, there is the peculiarity that the sporangial wall is more massive, consisting of 4-7 layers. Putting such differences aside there seems reason to regard the single tangential series of archesporial cells as a common feature of the sub-genus *Urostachya*; further, the sporangia are inefficiently protected by the sporophylls (Fig. 183, g, h, i).

In Pritzel's arrangement of the genus the section *Inundata* is separated from *Phlegmaria*, and placed in the second sub-genus *Rhopalostachya*. The sporangial character upholds this change. The sporangia are from the first more bulky than in *Urostachya* (Fig. 185, k, l, m). The sporangium of *L. inundatum* as seen in radial section arises as a broad swelling, while two cells have been seen to divide periclinally, indicating at least two tangential rows of archesporial cells in place of the single row in *L. Selago*. This origin of the sporogenous tissue may still be traced in the older stages (Fig. 184).

Of the rest of the sub-genus *Rhopalostachya*, *L. clavatum* and *L. alpinum* have been examined, and they both show a still more massive type of sporangium. This is seen in the mature state (Fig. 185, q, r, s, t, u, v, w), where the stalk appears to be short and thick; moreover, it is seen that the strobilus is constructed in these species so as to afford more complete protection to the sporangium while young, than is the case in the simpler type of *L. Selago*. This is effected by special development of the lower parts of the sporophylls (Fig. 150, D, E); in some cases, as in *L. cernuum*, the sporophyll takes a peltate form: it is often dry and chaffy in texture, but well provided with stomata, though photosynthesis is reduced or absent. Radial sections of the young sporangium show, both in *L. clavatum* and in *L. alpinum*, that from the first

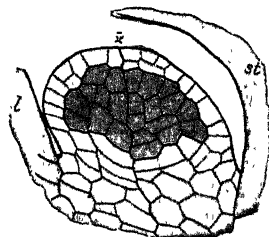


FIG. 184.
Lycopodium inundatum, L. Radial sections of sporangia. In the upper, younger sporangium periclinal divisions are shown in two cells, and the archesporial cells are shaded. In the lower, older figure the product of division of these cells is shown. $\times 200$.

at least three cells in each radial section are involved in the origin of the archesporium, sometimes even more than three (Fig. 186, *A, B*). Occasionally

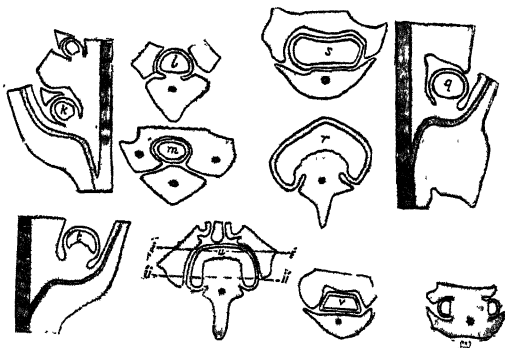


FIG. 185.

Drawings to illustrate the form and manner of protection of the sporangia in the sub-genus *Rhopalostachya*, of *Lycopodium*. *k, l, m*, sections of *L. mundatum*; *q, r, s*, of *L. alpinum*; *t, u, v, w*, of *L. clavatum*. $\times 12$.

periclinal divisions appear in the superficial cells, by which subsequent additions may be made to the archesporial tissue (Fig. 186, *B*, cells marked *x*). The tangential sections also show an advance on the *Selago* type : for twelve

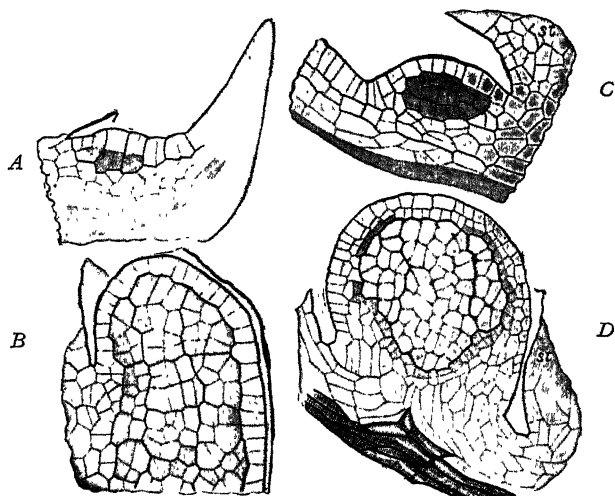


FIG. 186.

Lycopodium alpinum, L. *A*=Radial section through a sporophyll and young sporangium. *B*=the same, older; in both the sporogenous tissue is shaded. *D*=radial section of an older sporangium; *st*=stem. *C*=tangential section of a sporangium of *Lyc. clavatum*, of similar age to *D*; in both these figures the sporogenous tissue is referable in origin to three rows of cells. *A, B, C* $\times 200$. *D* $\times 100$.

is not an uncommon number of the archesporial cells in one tangential row as against seven in *L. Selago*, or five in *L. Phlegmaria*. Countings of the sporogenous cells laid bare in sections of these bulky sporangia at an age

approaching the tetrad-condition show that their number is far in advance of those of the *Selago* type (Fig. 186, *C, D*); moreover, their thicker and shorter stalks would be well fitted to transfer the necessary nourishment for the larger spore-output. Thus in the main features of form and dehiscence the sporangia of *Rhopalostachya* conform to the type of *L. Selago*, but are larger and more productive; while the sporophylls have a more elaborate form for purposes of protection. This goes along with the differentiation of the vegetative from the propagative regions, the steps of which have been traced above in the genus *Lycopodium*, as indicating an advanced organisation.

The strobilus of *Phylloglossum* resembles that of the sub-genus *Urostachya*, rather than that of *Rhopalostachya*. An examination of the develop-

ing sporangium supports this comparison, for only a single row of about six archesporial cells is found; but, on the other hand, the outline of the sporangium, and the relative thickness of the stalk, show some similarity to *L. inundatum*.

The sporangium of *Selaginella* corresponds in general type to that of *Lycopodium*. It is usually described as arising from the surface of the axis: in some species it does so (*S. Martensii*) (Fig. 187), but in others it is seated more nearly upon the surface of the leaf.

There has been considerable divergence of opinion as to the details of its development, which not improbably arose in part

from want of exact uniformity in different species, partly from difficulty of observation, owing to the small size of the cells in young stages. *S. spinulosa* is among the least differentiated species as regards external form, and on that account it deserves special attention. The description here given will be based on that species. According to Goebel the whole sporogenous tissue, as seen in the radial section in *S. spinulosa*, is referable in origin to a single archesporial cell, which is, however, one only of several forming a tangential series. This may sometimes be the case; but as a rule two primary archesporial cells have been seen (Fig. 188, *A, B*), somewhat as in *Lycopodium inundatum*. Tangential sections show that these represent two rows of archesporial cells, with about four cells in each (Fig. 188, *D*). The correspondence in sporangial type with that of *Lycopodium* is very striking, as regards early development: the chief difference is in the origin of the tapetum, for this in *Selaginella* is cut off by tangential divisions from the sporogenous tissue (Fig. 188, *C, E*), of which it is thus a sterilised part.

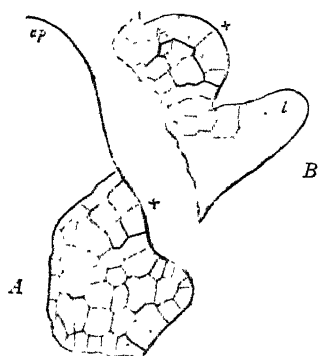


FIG. 187.

Selaginella Martensii, Spring. Sporangia in radial section. *A* traverses the stem apex (*ap*), the sporophyll (*l*), and sporangium (*x*); in the latter two archesporial cells are seen, shaded. *B* shows an older stage. $\times 350$.

In the microsporangia all the cells of the sporogenous group may undergo the tetrad-division, and form microspores ; but sometimes only a small proportion are fertile, the rest disappear. In the megasporangia, as a rule, a

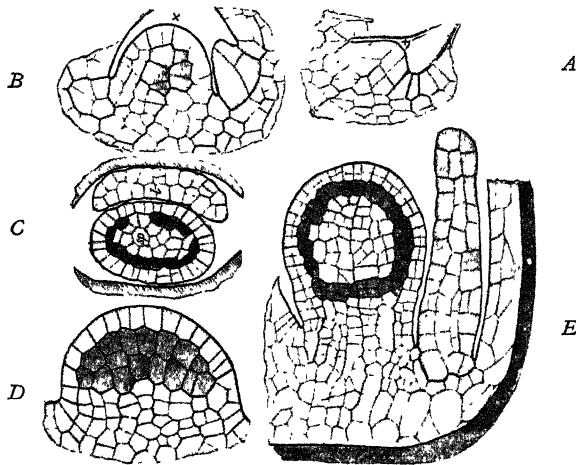


FIG. 188.

Selaginella spinulosa. A, B=radial sections through young sporangia of successive ages. C=a transverse section of one more advanced. D=a tangential section. E=a radial section of an older sporangium showing all its essential parts, together with the ligule and part of the sporophyll. A, B, C, D $\times 350$. E $\times 200$.

single cell is early differentiated by its denser protoplasm from the rest : this alone undergoes the tetrad-division, and forms megaspores, and the number four is the most usual for the genus (Fig. 189). But in *S. rupestris* a smaller number of megaspores, or even one only, may come to maturity. There is, in fact, great variety within the genus both in their number and in their size. Such numbers as 6, 8, 12, 16, 36, and even 42 megaspores have been noted. The highest figures are recorded for *S. Willdenovii*, in which species also their size varies greatly, though constantly in excess of that of the microspores (Fig. 190) (Duerden, *Ann. of Bot.*, xliii., p. 452). These fluctuations have their bearing upon the origin of the heterosporous differentiation, showing that there is a wide margin of variation in the number of spore-mother-cells which are fertile even in forms now living.

The facts relating to the sporangium in *Selaginella* show that in position and in general plan the sporangium is of the usual Lycopod type, but that

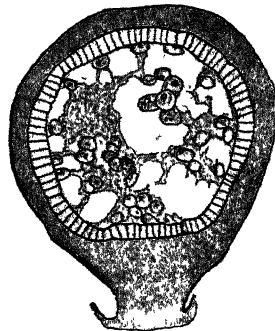


FIG. 189.

Selaginella spinulosa, A. Br. Section of megasporangium showing the single fertile tetrad still very small, and the rest of the sporogenous cells arrested. $\times 100$.

its dimensions are smaller than usual in *Lycopodium*; the difference in origin of the tapetum is probably related to the smaller size of the whole sporangium. The heterosporous condition appears to have brought with it only minor modifications of the original sporangial type. The adult sporangia of *S. apus* are shown in vertical section in Fig. 191, *A*, *B*.

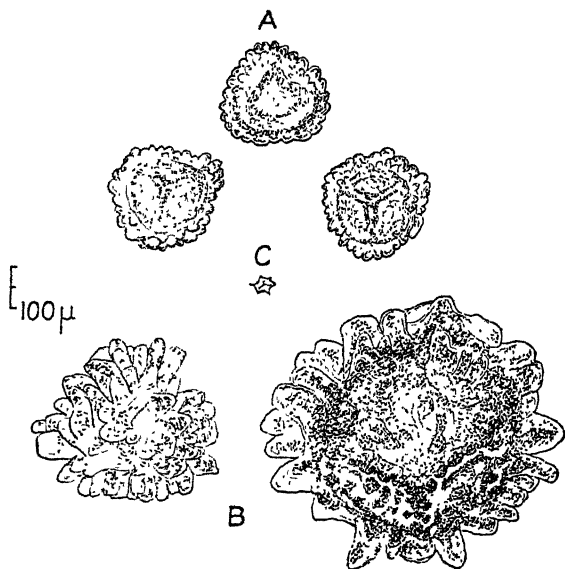


FIG. 190.

A, Three megaspores from a sporangium containing 24 spores. *B*, two megaspores from a normal sporangium. *C*, a microspore. All from *S. Willdenowii*. (After Duerden.)

Though the sporangia of the Lycopods conform to a relatively constant type, they differ in efficiency for scattering the spores (Von Goebel, *l.c.*, pp. 1334-1339). In *Lycopodium*, though a distal slit in a plane parallel to that of the sporophyll is determined by a tract of thinner-walled cells, no active ejection of the spores has been observed. Such movements of opening and closing as have been seen are due to a simple cohesion-mechanism, which affects the slit passively. But in *Selaginella* both microsporangia and megasporangia eject their spores forcibly—the latter with great vigour. Here a hinge-like band of thin-walled cells, along each margin of the purse-shaped capsule, allows of a change of form in the two valves, the cells of which are indurated. At ripeness these valves flatten, and their cohesion-mechanism presses so strongly on the megaspores within that these are shot out to a considerable distance. One effect of this is simply their distribution; but a second consequence is that the megaspores may fall in juxtaposition with microspores from another source. Obviously the risks of failure of such a relation are greater than if the spores were quietly shed; but this is sometimes met by the formation of apogamous sporelings.

In *Isoetes* the position of the large sporangium, between the ligule and the axis, corresponds to that in *Selaginella*, though it is here definitely inserted on the leaf-base, and is sunk in a deep depression of its upper surface (Fig. 164, *B*, *C*, *D*); but these differences of detail do not obscure the essential unity of the plan in the two genera. Instead of being a body more or less flattened between the sporophyll and the axis, as in *Lycopodium* and *Selaginella*, the sporangium is here extended radially outwards from the axis into a broad cake-like body. It may best be regarded as a result of such variation of dimensions as has been seen in minor degree within the genus *Lycopodium*,

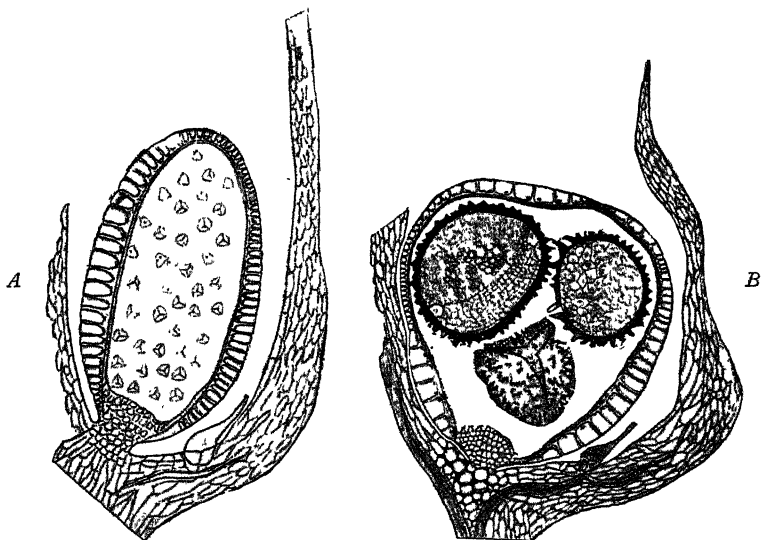


FIG. 191.

Sporangia of *Selaginella apus* in vertical section, together with the ligule and sporophyll. *A*, a microsporangium with numerous microspores. $\times 55$. *B*, a megasporangium, showing three of the four megaspores. $\times 21$. (After Miss Lyon.) In order to appreciate the full difference in size the difference of magnification should be noted.

but here carried to greater lengths. The developmental details harmonise readily with this view. The microsporangium is naturally a better basis for comparison with the homosporous Lycopods than the megasporangium, and it will therefore be taken first. The mature structure of a microsporangium is shown in Fig. 164, *D*, which indicates how the very large internal space is traversed by sterile trabeculae: these extend, with many irregularities of branching and wing-like expansions, which are not shown in the figure, from the sub-archesporial tissue to the covering wall. The type of the megasporangium is the same, though the trabeculae are here fewer in number but more massive, so that the proportion of sterile tissue to the fertile is much larger in the megasporangium. As the development shows, the trabeculae have a common origin with the fertile sporogenous cells; there has in fact been a sterilisation of potentially fertile tissue, which proceeds to a greater

length in the megasporangium than in the microsporangium. The early development of both types of sporangia is alike up to a fairly advanced condition, as is the case also in *Selaginella*; this fact has its bearing on the origin of their differentiated state.

The sporangium of *I. lacustris* originates from superficial cells of the leaf-base of small number, lying below the ligule (Fig. 192, *A*). The cell seen immediately below the ligule in the longitudinal section of the young leaf forms the velum: the rest show some evidence of common origin by earlier

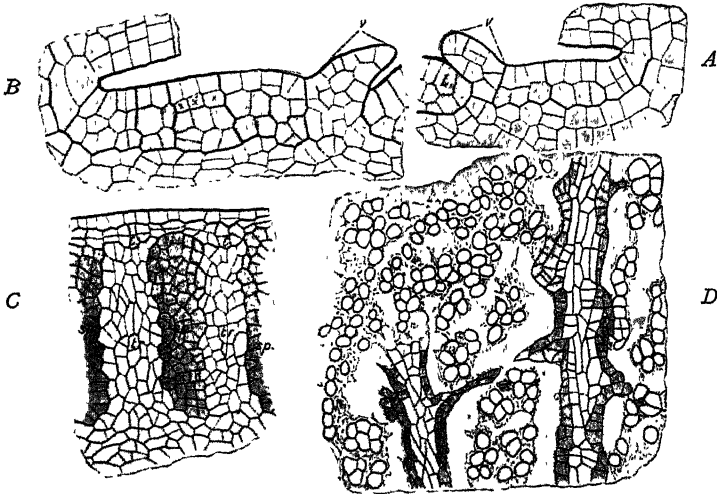


FIG. 192.

Isoetes lacustris, L. *A*=radial section through base of sporophyll with ligule (*l*), velum (*v*), and sporangium, in which the archesporium is shaded. *B*=a similar section of an older sporangium. *C*=part of an older microsporangium, showing the potential archesporium differentiated into trabeculae (*tr*), and sporogenous tissue (*sp*), while the tapetum (*t*) is clearly defined. *D*=an older stage with spore-mother-cells separated, and tapetum shaded covering the trabeculae. *A*, *B* $\times 200$. *C*, *D* $\times 100$.

anticlinal segmentation; this may very well have been so, but the comparative interest begins with their periclinal divisions, which appear first in the central part of the young sporangium and thence extend in either direction; in the longitudinal section some four or five cells are involved in *I. lacustris*, though apparently the number may be smaller in *I. echinospora*. Comparing this with the condition as seen in *Lycopodium* it appears to be an advance on even the most complex type, such as *L. alpinum* (Fig. 186); and this accords with the radially extended form of the mature sporangium of *Isoetes*.

The internal cells thus cut off by the first periclinal divisions are destined to be sporogenous. The tissue thus produced, after successive sub-divisions, forms a very considerable sheet of tissue, several cells in thickness. Of this, however, only a portion develops into spores; in the case of a microsporangium certain tracts of cells of this tissue assume dense protoplasm, and the cells, ultimately separating from one another, undergo the tetrad-division,

producing microspores (Fig. 192, *C, D*); but other tracts of cells, not referable in origin to predetermined cells of the genetic tissue, become less densely protoplasmic and form the sterile trabeculae. A tapetal tissue invests the fertile tracts: it is derived partly from the innermost layer of the sporangial wall, as in *Lycopodium*; partly from the superficial cells of the trabeculae. A similar differentiation of the potentially sporogenous tissue is found also in the megasporangia, the early stages of which are quite indistinguishable from those of the microsporangia; but in the former a relatively smaller number of isolated cells, distributed with no constant relation to their ultimate parent cells, enlarge and divide to form the megaspores (Fig. 193). There is no opening mechanism in the submerged sporangium of *Isoetes*. The study of their development thus leads to the conclusion that there has been a differentiation, within the sporangia, of tissues at first of uniform character: that part of the potential sporogenous tissue remains fertile, but a large proportion in the microsporangium, and a still larger proportion in the megasporangium, is diverted to other uses, and remains sterile. There is clear correspondence to the Lycopod-type, and especially to those forms with the more bulky sporangia. If we imagine a heterosporous Lycopod, with its sporangium extended radially along the leaf-surface and its enlarged sporogenous tissue partly sterilised so as to form trabeculae, the result would be practically what is seen in *Isoetes*.

A study of the sporangia of the fossil Lycopods is a necessary adjunct to that of the modern forms, though the usual absence of developmental details in them restricts the comparison to the basis of mature structure. On this footing it appears that the type of sporangium characteristic of the sub-genus *Urostachya*, and showing special resemblance to that of *Lycopodium Phlegmaria*, dates back at least to the calciferous sandstone, for it is seen in *Lycopodites Stocki* (compare Fig. 154). Sporangia apparently of the same type have been recognised also in other early fossils referred to *Lycopodites*, but their small size and the state of preservation do not allow of any exact comparison. Of other apparently non-ligulate types one of the best

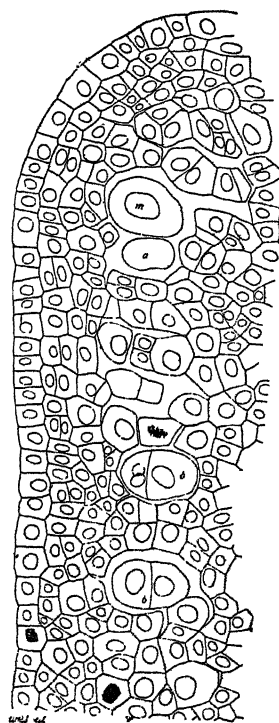


FIG. 193.

Part of a section of a megasporangium of *Isoetes*. The cell marked (*m*) is the only fertile spore-mother-cell; the rest are undergoing vegetative divisions, including the cell (*a*), as shown by other sections of the series. Thus sterilisation affects the large majority of the cells of the sporogenous group. $\times 245$. (After Wilson Smith.)

known as regards the details of the strobilus, though its vegetative region is still unknown, is *Spencerites* (Fig. 194), which has been described by Scott and others from specimens from the Coal Measures, showing microscopic structure. Here the verticillate or spiral sporophylls consist of a narrow pedicel bearing an upturned lamina; at the base of the lamina is a massive ventral outgrowth, to which the sporangium is attached by a narrow neck. There is also a thick dorsal lobe below, inserted opposite to the ventral one. The presence of the

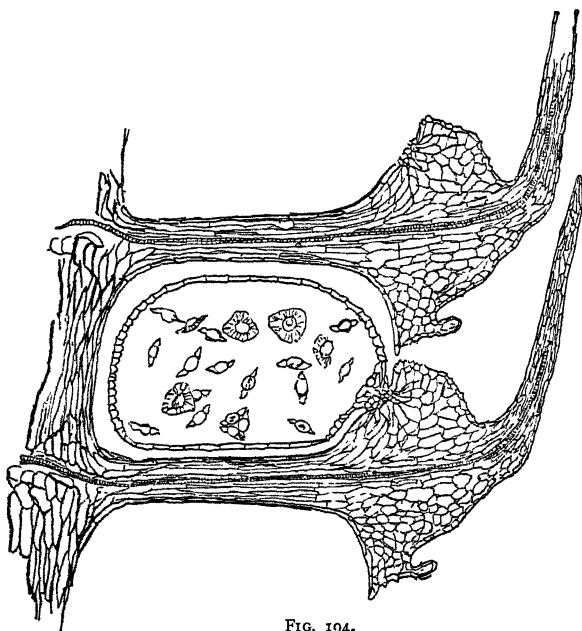


FIG. 194.

Spencerites insignis. Somewhat diagrammatic radial section of part of the cone, showing two sporophylls in connection with the axis. On the lower sporophyll the sporangium is shown attached at its distal end to the ventral outgrowth of the sporophyll: within the sporangium some of the characteristic winged spores are shown. (After Miss Berridge.) From Scott, *Progressus rei Botanicae*, vol. 1.

ventral sporangiferous lobe has suggested a comparison with the Sphenophyllales, though the absence of any vascular supply renders the analogy somewhat remote. It is doubtful what is the evolutionary relation between the distal and the basal insertion of the sporangium upon the sporophyll, as seen in the Lycopodiales. But such differences as these are of degree only, in a type which is constant as regards the numerical relation of the sporangia to the sporophylls, and in the coincidence of the median planes of both of those parts. There seems little reason to hold that these peculiarities of *Spencerites* are archaic. Stratigraphically the ordinary Lycopod type is quite as early as *Spencerites*.

The apparent absence of a ligule, and of any evidence of heterospory in *Spencerites*, together with the simple structure of the adult sporangial wall,

are facts which point towards an affinity with the Eligulate Lycopods. This question has been considered by Lang, who compares the fossil with *Lycopodium cernuum* (*Proc. R.S. Edin.*, vol. xxviii., 1908, p. 356). He concludes that there is a *prima facie* case for regarding the cone of *Spencerites* as having been constructed on essentially the same plan as that living species. Moreover, he observed that in the living species the region between the insertion of the sporangium and the axis of the cone is intercalated late in the ontogeny, and the case may have been the same in the fossil. It thus appears that *Spencerites* finds its best place with the Eligulate Lycopods, notwithstanding the peculiar form of the sporophyll and the position of the sporangium (Sykes, *New Phyt.*, vii., 1908, p. 41).

The same general relation of sporangium to sporophyll as is seen in the living Lycopods is maintained in the Lepidodendroid cones, which are known

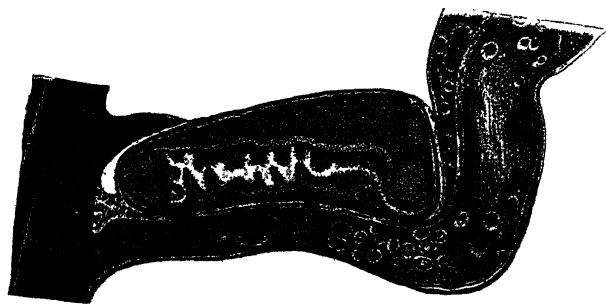


FIG. 195.

Lepidostrobus Brownii. A radial section traversing the axis, a sporophyll, and a sporangium. In the latter numerous spores are seen partially filling it, while sterile processes project upwards into the cavity. (From Sowerby's drawing.)

in many cases to bear ligules, and to be heterosporous, thus corresponding more especially to the Ligulate series of the Lycopodiales. An examination of the details of the sporangium should naturally be carried out in the best preserved specimens, though these may not be typical of all others. *Lepidostrobus Brownii*, Schpr., is probably the best preserved of Lepidodendroid cones, and it will therefore be taken first. The large silicified specimen in the British Museum was first described by Robert Brown, with drawings by Sowerby (*Linn. Trans.*, vol. xx.). The original specimen was evidently only the upper part of a strobilus: and it has since been shown by Zeiller that the base of the cone is preserved in Paris; and that while the upper portion bears microsporangia the lower bears megasporangia (*Mém. de l'Acad. d. Sci. Paris*, 1911). He has also demonstrated the presence of a ligule. Thus this large and well-preserved cone compares in all essentials with numerous other Lepidodendroid cones, and ranks with them as the strobilus of a large Ligulate and heterosporous Lycopod. It measured about 5 cm. in diameter and about 12 cm. in length. The central axis shows a structure similar to that of *Lepidodendron Harcourtii* (Fig. 174), and there is no doubt of its

being the strobilus of a *Lepidodendron*. The axis bears numerous whorled sporophylls, of which about thirteen are represented in each transverse section: the basal region of each extends horizontally from the axis, and supports the sporangium, which may extend for fully half an inch along its surface (Fig. 195). The distal end of the sporophyll turns upwards, without any peltate expansion.

Comparison of transverse and tangential sections of the cone (Fig. 196, *B, C*) gives a clear idea of the form of the very large sporangium, which is

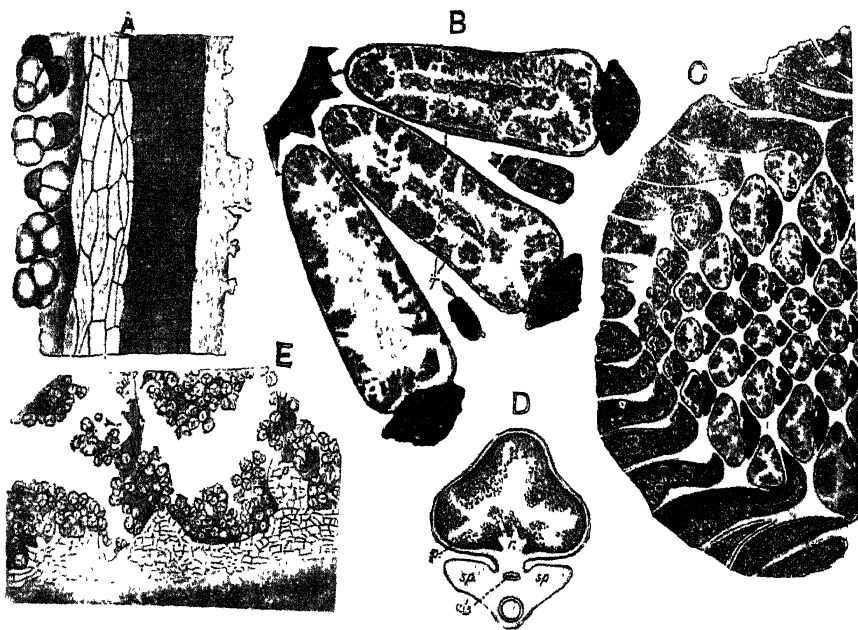


FIG. 196.

Lepidostrobus Brownii. *A*=wall of sporangium, showing outer sclerotic cells (*sch*), with several thin-walled layers within. $\times 100$. *B*=three sporangia in transverse section of the cone; *r*=median ridge. $\times 3$. *C*=cone in tangential section. *D*=sporangium in tangential section of cone, slightly diagrammatic; *sp*=sporophyll; *r*=sub-archesporial ridge; *v*, *b*=vascular bundle; *p*=processes rising from the ridge. $\times 6$. *E*=small part of the base of a sporangium in radial section, showing the processes *p*, *p'*, which rise from it. $\times 20$.

a radially extended body, broader and deeper at the distal end than at the proximal; it is attached throughout its length by a relatively narrow median, flange-like insertion to the upper surface of the sporophyll, and lies immediately above the course of the vascular bundle. Comparison of its outline with that of the sporangium of *Isoetes* shows a very striking similarity; but this is not limited to the form only. In *L. Brownii* above the flange of insertion an internal ridge of sterile tissue extends upwards into the sporangium, just as in *Isoetes* (*r*, Fig. 196, *B, D*), while from it sterile processes project further upwards, rising far into the cavity, and traversing the mass of the

spores (*E*). In the mature sporangium they stop short of the upper sporangial wall, but in the young state—as seen in the arrested sporangia towards the apex of the cone—they may extend completely across the cavity: in position and in number they are irregular, as are the trabeculae of *Isoetes*, to which they show a striking similarity. It seems probable that they are truly comparable to the trabeculae of *Isoetes*. The large cavities of the microsporangia are filled with small spores, arranged in tetrads, and it is probable that the trabeculae were of importance in the nourishment of the large sporogenous mass, as also mechanically. The wall of the sporangium in *L. Brownii* consists of an outer layer of indurated prismatic cells, supported by four or more layers of thin-walled cells (Fig. 196, *A*). The points of similarity of this remarkable fossil to the fertile plant of *Isoetes* strongly support the view that the plant of *Isoetes* is like a stunted *Lepidodendron*.

In other *Lepidostrobi* the general form of the sporangium is the same as that above described: there is great radial extension, while in a number of them a ligule has been found at the distal end, thus corresponding in position to that in *Isoetes*. The

sporophylls of some of them are liable to peltate expansion at the apex: they are then so disposed that the downward-turned lips of the upper sporophylls are enveloped by the upturned lips of the lower, thus giving very complete protection to the sporangia. This may be held to be a secondary adaptation of their form, comparable to that seen in some of the more specialised cones of *Lycopodium* belonging to the sub-genus *Rhopalostachya*, while in the simpler *Selago*-forms the sporophylls are as in *L. Brownii*. The wall of the mature sporangium is frequently represented by the single prismatic outer

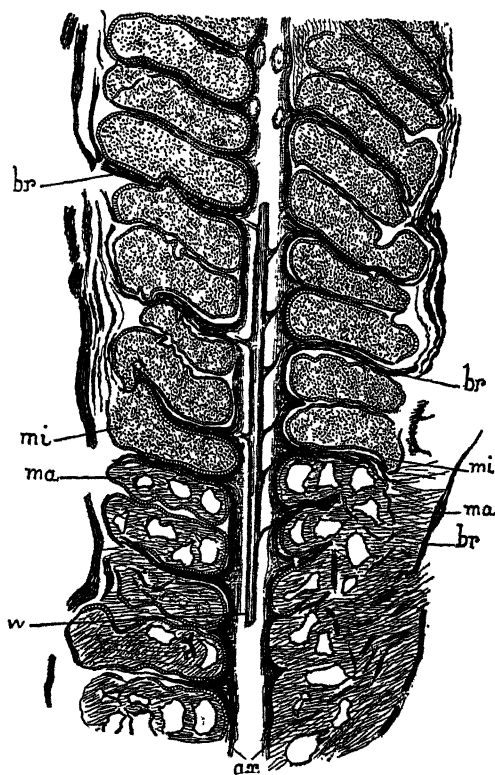


FIG. 197.

Lepidostrobus Veltheimianus. Longitudinal section of cone, showing microsporangia above and megasporangia below. *ax*=axis of cone, showing stele, *w*, and leaf-traces, passing out to sporophylls, *br*; *mi*=microsporangia; *ma*=megasporangia containing a few spinose megasporos. \times about 4. (From Scott's *Studies in Fossil Botany*.)

layer alone, the inner thin-walled layers seen in *L. Brownii* being absent; this difference is comparable to that seen in *Lycopodium*, where the mature wall usually consists of a single layer, but in *L. dichotomum* of several layers. There is also some divergence in detail of the internal upgrowths from the basal ridge: in most *Lepidostrobi* these take the form of longitudinally disposed plates, of which one or more project upwards into the sporangial cavity. Lastly, there is the fact of heterospory, which has now been established in a number of examples, though it must not be assumed for them all without actual demonstration (Fig. 197).

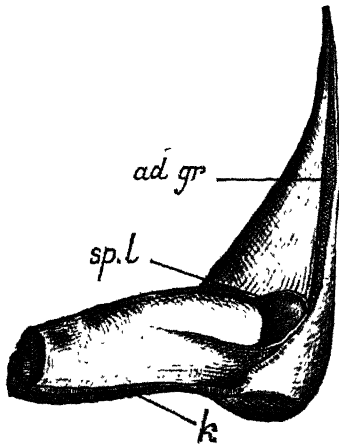


FIG. 198.

Diagram of the sporophyll and megasporangium of *Mazocarpon*, from a model by Dr. M. Benson. *ad. gr.*, adaxial groove of sporophyll; *k*, keel; *sp. l.*, distal lamella of the sporangium. (From Scott.)

The fructifications of *Sigillaria* appear as cones sometimes sessile, but more commonly borne on long lateral branches, which are covered below with acicular bracts: such strobili are thus more strongly differentiated from the vegetative axes than is the case in *Lepidodendron*. The plan of construction of the cone itself appears to have been the same, and though its preservation is commonly imperfect, it seems that the sporangia of *Sigillaria* resembled those of *Lepidodendron* in their form and mode of insertion, as also in the existence in them of a heterosporous condition. They were sometimes of large dimensions: frequently, however, of smaller size. Among them a small cone, described by Zeiller as *Sigillari-*

ostrobus Crepini, differs from the rest in the distal insertion of the sporangium upon the sporophyll, corresponding in this respect to *Spencerites*.

Under the name of *Mazocarpon* a fossil of Lycopod type has been described, which has been traced back from the Coal Measures to the Calcareous Sandstone. It has been referred to *Sigillariostrobus* by Dr. Benson (*Ann. of Bot.*, xxxii., p. 569). Both megasporangia and microsporangia are known, but the chief interest is in the former. A massive, radially extended megasporangium is attached to the upper side of the sporophyll, and its wall is produced into a thin distal flange. The most distinctive feature is that the basal ridge, or sub-archesporial pad, is persistent, and developed so as to occupy all the middle region of the sporangium, and even to connect with the outer wall, which is thick and durable. Transfusion-tracheides extend from the vascular strand of the sporophyll upwards into the sterile tissue, while the large megasporangia, some eight in number, are embedded in it (Fig. 198). The megasporangium with the remains of the bract became readily detached at

ripeness, and it seems to have broken up naturally into fragments. Here is something more advanced than in *Lepidostrobus*, the main feature being the extended sterile tract, with its transfusion-tracheides. Nevertheless, the underlying type is distinctly Lycopodioid, and the structure shown is readily ranked as a physiological amendment upon such structure as is seen in *Lepidodendron* or *Isoetes*. On the other hand Dr. Benson states (*l.c.*, p. 577) that the microsporangia referred to *Mazocarpon* bear some resemblance to those of *Isoetes*: the structure suggests that the sterile parenchyma between the masses of microspores has been formed from potential sporogenous tissue.

Here mention may be made of a puzzling type known only by impressions, not by detailed structure. It was a large cone described as *Cantheliophorus*: it readily shed its scales, which with their appendages were of an elaborate type. The pedicellate base of the sporophyll, keeled on the abaxial face, projects at right angles to the axis, and bears a long narrow distal blade. On the adaxial face is an oblong elliptical body, described by Bassler as a "sporangiphore," bearing two elongated sporangia attached well forward from the axis (*Bot. Gaz.*, vol. lxviii., 1919, p. 73). The sporangia are seated pannier-like right and left, with an erect crest between them. Nathorst suggested, as an interpretation of the sporophyll and its appendages, that "we may be dealing with a sporangium in which longitudinal sterile plates, such as we observe in certain sporangia of *Lepidostrobus*, were developed to a point where they divide it into distinct and separate loculi: two loculi where the plate is simple, three where it forks." This seems to be a more probable interpretation than that given by Bassler, which was that the oblong body borne on the adaxial face of the sporophyll is of the nature of a sporangiphore. Since the microscopic structure is not known, opinion must remain in suspense, with a preference in favour of a sporangial rather than of a sporangiophoric reading of the facts so far disclosed. But meanwhile Dr. Benson sees in these impressions nothing more than the structure already observed in the microsporophylls of *Sigillariostrobus* (*Ann. of Bot.*, xxxiv., 1920, p. 135).

A brief allusion must also be made to those advances which lead to a seed-like habit in certain Lycopods. The biological effect is to minimise the chances of failure of fertilisation in heterosporous plants, by attaching the microspores relatively early in close relation to the megaspores; and so to escape the risks naturally following on a general dissemination of the spores. On the other hand, the retention of the megaspore within the sporangium, which is the essential feature of the seed-habit, brings the advantage of placing the physiological resources of the parent at the disposal of the embryo. A first step towards this double result is heterospory itself. A condition where the megaspores were shed separately, which involves the risks that face any modern *Selaginella*, appears already in *Bothrodendron* from the Upper Devonian, with its four or sometimes more megaspores in

each sporangium, which are duly shed (Fig. 199, *B*).¹ But in *Lepidocarpon* and *Miadesmia* only a single effective megaspore was produced in each sporangium, and it was retained there. Further, in *Lepidocarpon* an integument, arising relatively late in the form of two lateral flaps originating from tissue of the sporophyll, enveloped the sporangium, leaving an elongated slit which served as a micropyle (Fig. 199, *A*). The seeds thus constituted fell away at maturity, together with the remains of the sporophyll. In *Miadesmia*, a *Selaginella*-like type, the integument formed a complete investment, except at the apex: and there it bore tentacles, which may have served for

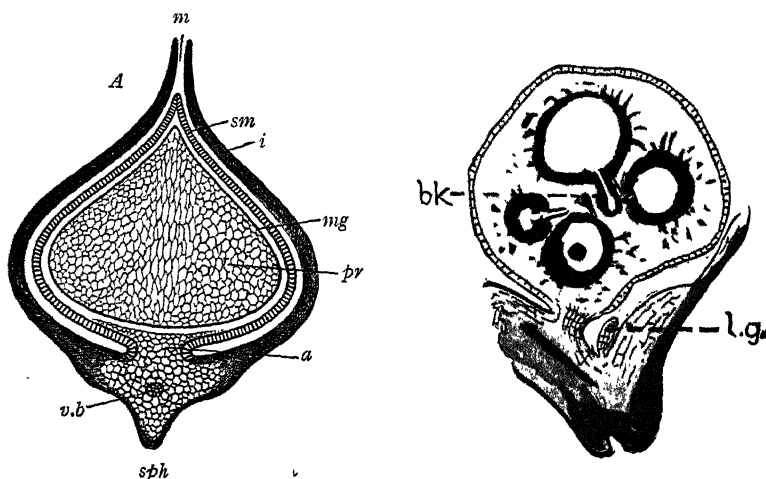


FIG. 199.

A, *Lepidocarpon lomavi*: diagrammatic section of the "seed," tangential to the cone: *sph*, sporophyll; *v.b*, vascular bundle; *i*, integument; *m*, micropyle; *sm*, wall of sporangium; *a*, base of sporangium; *mg*, membrane of megaspore; *pr*, prothallus. (After Scott.) *B*, *Bothrodendron mundum*. Sporophyll and sporangium in radial section. Four megaspores are shown. *bk*, beak of a megaspore; *l.g*, ligule of sporophyll. × about 30. (After Scott.)

retaining the microspores, thus securing fertilisation, as in some modern *Selaginellas*. All this falls in readily with progressive elaboration from the typical Lycopod sporangium, with its subtending sporophyll.

For further details of the fossil Lycopods reference must be made to works on Palaeobotany, such as Scott's *Studies in Fossil Botany* and the *Handbuch* of Hirmer.

The salient features in the fertile tracts of the Lycopodiales are the constant numerical relation of sporangium and sporophyll, their median planes coinciding. But the point of insertion of the sporangium may vary along the median line: in most of the Lycopodiales it is near to the axis; or it may even be inserted upon it, as in *Selaginella*; or, again, it may be

¹ Holden, *New Phyt.*, xxxi., p. 265, 1932.

inserted at the distal end of a pedicellate base of the sporophyll, as in *Spencerites*. These differences may be held as of secondary importance, so long as the median position is regularly maintained. Such extreme conservatism in number and relative position of sporangium and bract is peculiar to this Class among the Pteridophyta: the constancy may probably arise from a long phyletic history, with some deep-seated physiological advantage.

Notwithstanding the rigid maintenance of this relation of bract and sporangium the Lycopodiales present variations of structure and proportion of both, and extremes were attained early in the geological history in certain representatives of the Class. The simplest is the *Selago*-type, where the sporangium, only slightly flattened and fan-shaped, is inserted by a relatively thin stalk, while it is imperfectly protected by sporophylls little differentiated from the foliage leaves. In *Spencerites*, also, from the Coal Measures, the form of the sporangium was approximately spherical, and inserted by a narrow base, but at the distal end of the pedicel. This form of sporangium is shared by *Selaginella* among the Ligulate Series, and it is combined with heterospory, as it is also in *Bothrodendron* (Fig. 199, *B*). This shows that both features existed in the Coal Measures, and even earlier. It thus appears that sporangia of obconical form, only slightly flattened, and with cylindrical stalks, were of early occurrence, while they are represented both by Eligulate and Ligulate Lycopods of the present day.

Detailed comparative study of the development of the sporangium in *Lycopodium Selago*, *inundatum*, *clavatum*, and *alpinum* has shown that the archesporium may consist respectively of one, two, or three rows of cells tangential to the axis (Figs. 182, 184, 186). These facts introduce the conception of a progressive radial extension of the sporangium along the surface of the sporophyll, as seen in living Lycopods. It is accompanied by lengthening of the archesporial rows themselves, and an expanded, fan-like form of the sporangium. The result is an extensive archesporial sheet, giving potentially a greatly increased spore-output per sporangium. This progression marches as a rule, but not always, with increasing differentiation of the strobilus from the vegetative region, and a more perfect protection of each sporangium by bracts which have a reduced photosynthetic system, and by specialised flanges of various form (compare Figs. 185, 194). Such comparisons lead naturally to the Lepidodendroid type of sporangium, as seen also in the modern *Isoetes*. But the condition of a sporangium of large dimensions so constructed would present difficulties, whether mechanical or physiological, particularly at the period when the spore-mother-cells were floating free in a semi-fluid medium, and undergoing the most critical stages of their development. This is apparently one reason for further developments associated with a partial sterilisation of potentially fertile tissue. The result has been seen and traced developmentally in *Isoetes*: the trabeculae, particularly in the microsporangium, serve not only as mechanical

supports to the wide expanse of the thin sporangial wall, but also as purveyors, through the tapetum that covers them, of nutrition to the great volume of developing spores. The actual structure in *Lepidostrobus Brownii* offers a near parallel to what is present in *Isoetes*; particularly is it seen in the imperfect sporangia at the distal end of the cone, where the trabeculae are well preserved. In other cones of *Lepidodendroids* a median plate of sterile tissue, or sometimes more than one, projects upwards into the cavity of the sporangium, suggesting the possibility of partitioning. This was actually approached if not technically realised in the large sporangia of *Mazocarpon*, referred by Dr. Benson to *Sigillariostrobus*. Finally, in the large sporangia described as *Cantheliophorus* by Bassler, his description suggests the interpretation of them given by Nathorst, that septation of each into distinct sacs was actually complete.

Such structural advances were accompanied by the formation of a velum in *Isoetes*, and various flanges from the sporangial wall or from the sporophyll itself: such as the "sporangial lamella" in *Mazocarpon*, the "crest" in *Cantheliophorus*, and, in particular, the integument in the seed-bearing *Lepidocarpon* and *Miadesmia*. These growths all appear as parts of an advancing complexity based upon the simple Lycopodioid scheme. The evolution of the propagative system in the Class appears to have proceeded by exploiting the individual sporangium with its subtending sporophyll in an upward scale, starting from a simple, almost spherical and stalked head.

One of the most constant features in the whole history of the Lycopodiales has been that, notwithstanding the elaborations thus described, the single vascular strand of the sporophyll has maintained its identity throughout. The only exception appears to have been that of the leaf in *Sigillariopsis* where the strand is divided into two; but even these fuse at the distal tip (Scott, *l.c.*, Fig. 101).

CHAPTER XIV

PROTHALLUS AND EMBRYO OF THE LYCOPODIALES

OF all the Pteridophyta now living the Lycopodiales (in which till late years the Psilotales were habitually included) have seemed best to deserve the name of the "Higher Cryptogamia"; for while their sporophyte has for long been dealt with systematically the gametophyte remained till later days unknown. Even Hofmeister, who revealed so fully the completed cycle and sexual organs of other Archegoniatae, confessed that "the reproduction of those Lycopodiaceae which bear powdery spores of one kind only is still a mystery" (*Vergl. Unters.*, 1851: Engl. trans. 1862, p. 398). Repeated sowings yielded to him no result. But he records that De Bary had discovered in 1858 that the spores of *L. inundatum* produced a body composed of a few cells. These observations heralded a period of more than half a century, in which records of the prothalli, sexual organs, and embryos of many species of *Lycopodium* have gradually disclosed the life-story so long hidden from sight. Observations of a like nature for *Selaginella* and *Isoetes*, and even in some of the fossil Ligulatae, fill in the general picture for the Lycopodiales as conformable to that already known for other Pteridophytes. For *Lycopodium* itself it was natural that the facts should come slowly at first; for the prevalent saprophytic habit of the underground prothallus in European species hid it from ready observation, while the idea of mycorrhizic nutrition gave in earlier years no suggestion of any alternative to the green photosynthetic prothallus, as seen in Ferns and Equiseta. But the detailed descriptions now available serve to show that, notwithstanding the high degree of uniformity of the sporophyte of this cosmopolitan genus, there is in *Lycopodium* a wide range of variety of detail, both in the prothallus and in the embryo. Comparison suggests that within the genus the prothallus and embryo have undergone a cognate divergent development from a central type, in accordance with differences of nutritive method. This general outlook gives a special interest to the study of the differences of detail presented in *Lycopodium*, as well as in the closely related *Phylloglossum*.

PROTHALLI OF THE ELIGULATE LYCOPODIALES

Three main types of the prothallus within the genus *Lycopodium* may be distinguished which, however, graduate into one another in such a way as to

suggest their intimate connection by descent from some common source.¹ The first type shown by *L. cernuum*, and shared also by *L. inundatum*, *salakense*, and others, consists of a massive thallus, standing upright in the soil, of which the conical lower part is sunk while the upper part is exposed freely above ground, and is of a green colour ; in *L. cernuum* and *inundatum* it bears numerous irregular leaf-like lobes, though in *L. salakense* the lobes may be rudimentary or absent (Fig. 200). The prothallus is in the main a self-



FIG. 200.

To the right a young leafy plant of *Lycopodium cernuum*, L., with the prothallus, bearing its irregular assimilating lobes, attached on its left-hand side. \times about 20. (After Treub.)

nourishing body, though an endophytic fungus is almost constantly present, indicating a second but subsidiary line of saprophytic nutrition. As the prothallus grows a merismatic zone becomes localised surrounding the upper part of the cylindrical body, but below its apex : this contributes to the increase both of the upper and the lower regions, while above it the green expanded lobes are formed. The sexual organs appear between the latter, the youngest being nearest to the merismatic zone ; and the leafy sporeling plant, when formed, is attached laterally.

With this type the prothallus of *Phylloglossum* is to be associated, as described by Thomas in 1886, but without illustrations (*Proc. R.S.*, p. 285, vol. 69). The typical form, though subject to variations, consists of an oval

¹ The fundamental researches were those of Treub, *Ann. Jard. Bot. Buitenzorg.*, of the years 1884-6-8, and 1889 ; and later those of Bruchmann, 1898-1916.

tuber below bearing upwards a simple cylindrical shaft terminated by an expanded crown, on which the first sexual organs appear; below this is a

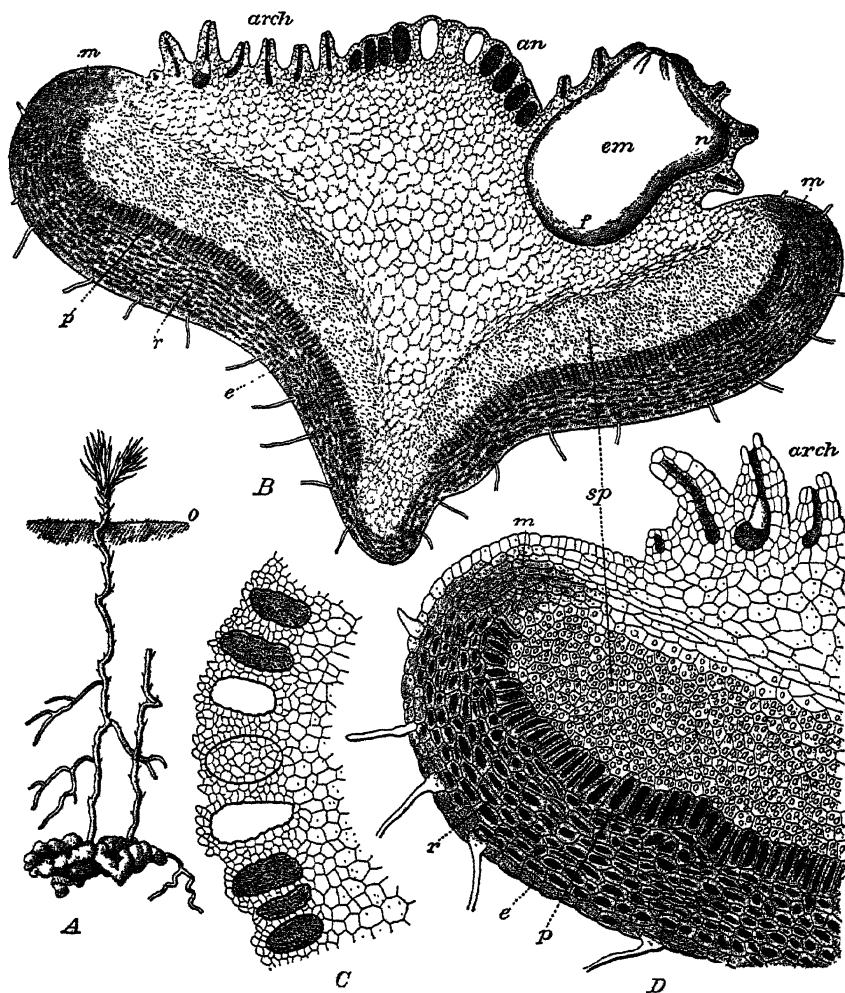


FIG. 201.

A=old prothallus of *Lycopodium annotinum*, L., with young plant projecting beyond the earth-surface (o). Natural size. B=median section through a young prothallus of *Lycopodium clavatum*, L., \times about 30. C=part of this from the middle region of the upper surface, with antheridia in different stages, \times 52. D=part of the margin of the median section, with meristem and archegonia, \times 52. e=the epidermis devoid of fungus, with rhizoids; r=cortical layers, with their cells filled by hyphal coils; p=the palisade layer, also filled with hyphae; sp=the storage tissue; m=the meristem; an=antheridia; arch=archegonia; em=an embryo; f=its foot; w=its root. (After Bruchmann, from Engler and Prantl.)

merismatic zone corresponding to that of *L. cernuum*. The whole upper part is green and photosynthetic, but there are no leafy lobes. An endophytic

fungus is present in the lower part, though there is little internal differentiation in relation to it, such as will be seen in *L. clavatum*, etc. On the whole the prothallus of *Phylloglossum* resembles that of *L. cernuum* more closely than any other. The embryo is attached laterally as in that species.

A second type shows in the ascendant that method of nutrition which was subsidiary in the first. It is exemplified by the large subterranean prothalli of *L. complanatum*, *clavatum*, and *annotinum*. In these the germination having been deep-seated, the massive prothallus is sunk in the soil: being thus shut off from the light it is colourless, and leaf-like lobes are absent. The lower region has a conical form, as in *L. cernuum*, the angle of the cone being wider in *L. clavatum* and *annotinum* than in *complanatum* (Fig. 201); its superficial tissues are, excepting the outermost layer, highly developed in relation to mycorrhizic nutrition (r, p), while the central region (sp) serves for storage. The conical base, which springs from the spore on germination, often widens greatly upwards, but its distal region flattens, finally becoming hollowed into a cup, owing to active growth of a marginal meristem (m). On the flattened or hollowed surface the sexual organs are formed, the archegonia being nearer to the margin and the antheridia being borne centrally. It thus appears that, even in an extreme form which is often irregularly lobed, the general plan is still the same as that in *L. cernuum*; while the embryo or embryos are produced laterally as a consequence of the position of the archegonia towards the lip of the cup.

A third type of prothallus is seen in *L. Phlegmaria*, and other epiphytic species. Here the form is attenuated and repeatedly branched, monopodially. The colourless cylindrical branches arise irregularly, at points distant from the apex of the main branch, and they extend widely through the dead bark in which the saprophytic prothalli grow, being attached by absorbent hairs which project in all directions (Fig. 202). The branches have a pronounced apical growth; normally there are two contiguous, prismatic initial cells, but their cleavages are not according to regular sequence. These give rise to an inner core habitually traversed by mycorrhizic filaments, and containing oil; it is enclosed by an external coat of one or more layers of cells, which are, as a rule, free from fungus. Such structure contrasts in detail with that of the *cernuum*-type, though its constituents are essentially the same. In particular the apical growth is here unlimited, and it is followed up by progressive decay. The result of this is a widespread development in the rotting bark, together with a generalised method of vegetative propagation of the gametophyte by the surviving tips of the branches. But propagation may also be effected by a production of gemmae that is often profuse, though localised. Near to the apex of a branch numerous shortly-stalked, pear-shaped bodies appear clustered together, and easily detached (Fig. 202, 1, 5, 6). They spring from single superficial cells of the branch, and in no regular sequence. The majority of the prothalli arise from these gemmae, not by

germination of spores. Again, on starved prothalli thick-walled gemmae with fewer cells may be formed; and being stored with nutriment they are able to survive through adverse conditions, and germinate when these are again favourable. Thus constituted and equipped the saprophytic prothalli of the *Phlegmaria*-type are well suited to their habitat; nevertheless the structure can be readily referred to the general Lycopod type.

The sexual organs of *L. Phlegmaria* are borne upon the upper surface of enlarged branches of the thallus, and the immediate presence of paraphyses

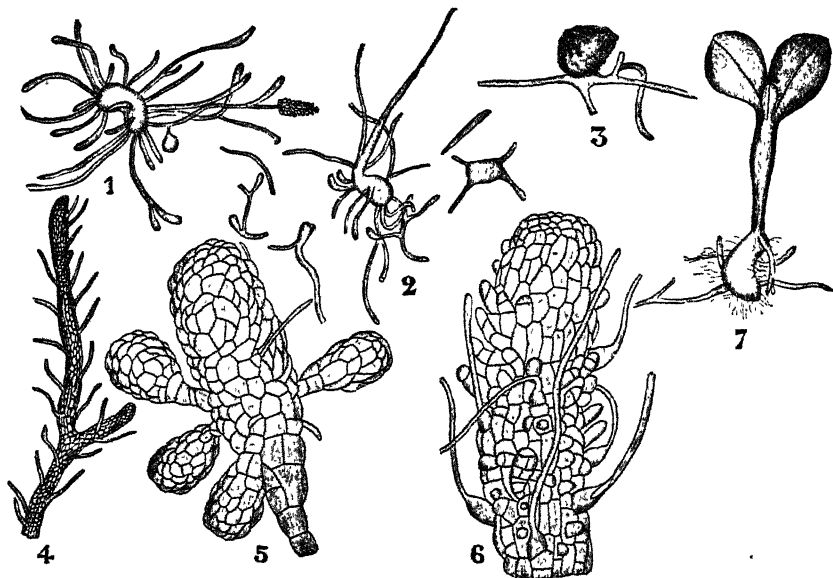


FIG. 202.

Lycopodium Phlegmaria. (After Treub.) 1, a complete gametophyte. In the middle the massive part bearing gametangia, from which a number of thread-like outgrowths arise; one to the right bears gemmae. 3, a separate outgrowth, which has formed a gametangia-bearing branch. 4, a sterile prothallus. 5, a gemma, bearing secondary gemmae. 6, tip of a prothallial branch, with rhizoids and young gemmae. 7, a prothallus with a young plant. (From Von Goebel.)

is a constant rule; this fact is exceptional not only in *Lycopodium*, but also in Pteridophytes generally. The structure and development of the antheridia and archegonia conforms to the *cernuum*-type. There is no constant local relation of these, but archegonia never appear unless preceded by antheridia; consequently fertile branches in the *Phlegmaria*-type are either hermaphrodite or male.

Such different types of prothallus as those described, when studied separately appear to be widely divergent, particularly in face of that degree of constancy which is shown in the features of the sporophyte. But comparison with the prothalli of certain other species serves to link them together: in particular the prothallus of *L. Selago* which was specially studied by

Bruchmann (1898, 1910). Lang (1899), who had also made observations on *L. clavatum*, pointed out clearly the relation of the divergent types to one general plan, recognising how the prothallus of *L. Selago* gives the clue to

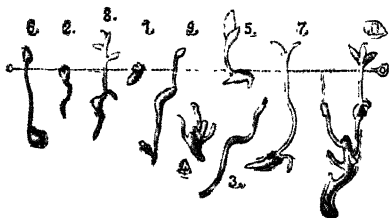


FIG. 203.

Prothalli of *Lycopodium Selago*, bearing sporelings. *o*, shows the level of the soil, and the sporelings in their development show varying proportions so that the first leaves shall be exposed above ground. (After Bruchmann.)

seems, in fact, to stretch upwards as though to bring to the surface a sporeling unsuited for subterranean growth. In more open soil, however, and especially near to the surface, the prothalli are more compressed and flattened. As in other types, they taper off below to a conical point, which indicates the

their connection. The prothallus of this species is usually a pale underground body, but it may also grow above ground, and it is then coloured a full green (Fig. 203). The spores appear to germinate either near to the surface or above it, and the form of the prothallus is determined largely by the depth and character of the soil in which it develops: an elongated cylindrical form is usually found in firm ground; the thallus

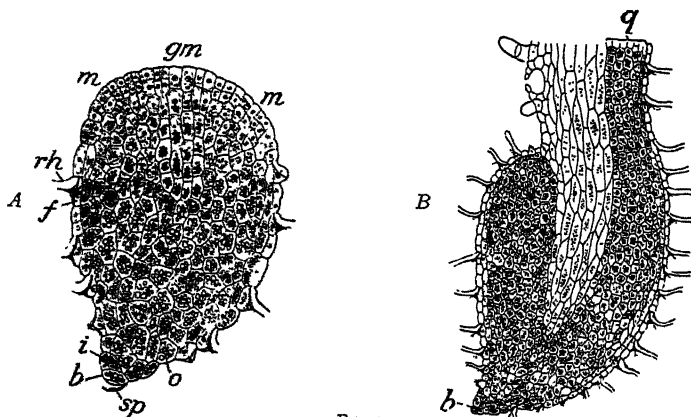


FIG. 204.

L. Selago. A, median longitudinal section through a young prothallus. *sp*=wall of spore; *b*=basal cell; *i*=mycelial filaments, and *o*=sporangioles within the cells; *rh*=rhizoids, and *f*=heel-like cells at the base of the hairs; *gm*=generative meristem. The rich store of starch in the central tissue is only indicated. (After Bruchmann.). B, Longitudinal section through an older prothallus, showing its radial region passing into the dorsiventral: *b*=the basal cell; *q*=the fungal region. The generative side bears an empty antheridium and paraphyses. Fungal filaments radiate out from each "heel-like" cell. (After Bruchmann.) $\times 125$.

origin from the spore (*b*, Fig. 204), while towards the upper end the sexual organs are formed. Bruchmann (1910) showed that here, as also in *L. clavatum* and other species, after the first steps of germination of the spore, the further vegetative development of the prothallus waits upon the advent of the endophytic fungus, as it does in the germination of certain orchids. This fact

accounts for the difficulty in raising the prothalli in cultivation. Special cells associated with the insertion of the rhizoids afford a ready connection between the endophytic fungus and the soil without (Fig. 204, *A*). The mycorrhizic zone in *L. Selago* is not so highly developed as in *L. clavatum* or *complanatum*; nevertheless it appears as a broad band surrounding a central clear core, which passes up to the apical region where the sexual organs are formed (Fig. 204, *A*, *B*). An interesting morphological feature in *L. Selago* appears in the transition from the radial structure which is general for the basal region of Lycopod prothalli to a dorsiventral structure. In *L. Selago* certain regions

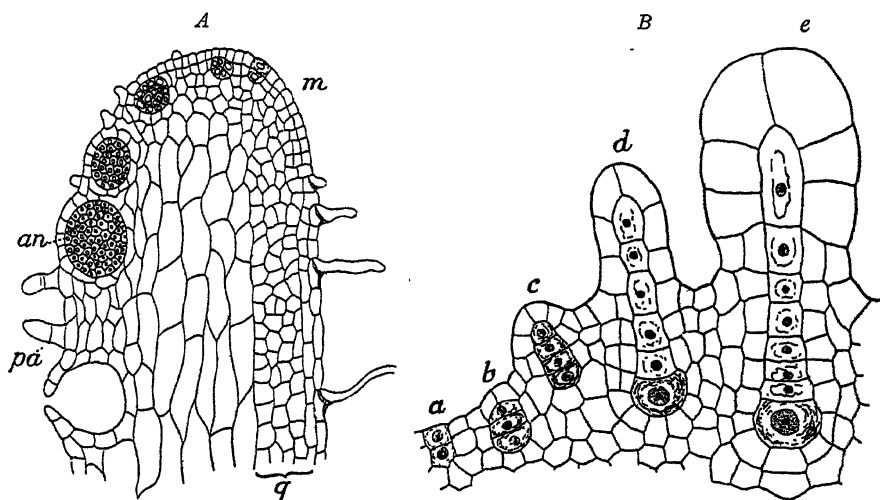


FIG. 205.

L. Selago. *A*, median longitudinal section through the dorsiventral process of a prothallus, bearing antheridia (*an*) and paraphyses (*pa*) on the generative side, while on the other is the fungal tract (*q*) with rhizoids. *m*=the meristem. $\times 250$. *B*, Archegonia seen in longitudinal section, in successive stages of development, *a* to *e*. $\times 270$. (After Bruchmann.)

of the margin of the distal cup grow out into thin flattened lobes bearing the sexual organs on one side only. The transition from radial to dorsiventral structure is seen in Fig. 204, *B*, and naturally the antheridia and archegonia are borne on the side of the lobe facing inwards, while the outward slope bears rhizoids (Fig. 205, *A*, *B*). Such a transition from radial to dorsiventral development of the gametophyte has its interest for comparison not only within this genus, but also elsewhere; in its course the original apical growth is replaced by a meristem situated at the margin of the cup, and this probably corresponds to the merismatic zone of the *cernuum*-type. Its activity is specially marked where the prothallus is exposed at the surface of the soil. The antheridia are disposed on the bilateral lobes in succession from the centre to the marginal meristem (Fig. 205, *A*, *m*). They are followed by numerous archegonia, succeeding one another till an embryo is formed (Fig. 205, *B*).

The sexual organs of *L. Selago*, which are typical for the genus, arise each from a single superficial cell, which divides periclinally, and the inner cell gives rise in the antheridium to the numerous sperms, in the archegonium to the canal-cells and the ovum (Fig. 205, *A, B*). As regards the length of the archegonial neck and number of the canal-cells *L. Selago*, with seven, takes a middle place between the short-necked archegonia of the exposed prothalli of *L. cernuum* and the long-necked archegonia, with eight to fourteen canal-cells, of the underground prothalli of *L. complanatum*.

It thus appears that, not only in their details but also in their fundamental structure, the prothalli of these several types of *Lycopodium* conform to one general plan: its fundamental form is obconical, the cusp of the cone corresponding to the spore from which it originates. The differences are readily intelligible in relation to the biological conditions. The chief divergent results are, (i) development at the surface of the soil with a tendency towards holophytic nutrition; (ii) underground development with dependence upon mycorrhizic nutrition, and a massive convoluted form; and (iii) epiphytic development with elongated specialisation to saprophytic life. Between these extremes of specialisation the prothallus of *L. Selago* takes a middle place as regards form and function, linking the others together, and indicating the conical, massive, upright, and radially constructed thallus with a balanced nutrition, in part mycorrhizic in part photosynthetic, as a central feature. From this type a feeble degree of dorsiventrality, represented in *L. Selago* and repeated in some other species, and a formation of irregular lobe-like appendages, as in *L. cernuum* and some others, are seen to emerge. How far such a central type as that of *L. Selago* has phyletic significance must remain open for later consideration.

EMBRYOGENY OF THE ELIGULATE LYCOPODIALES

There is divergence of detail also of the embryo in the Eligulate Lycopods, and it will be seen that the differences which they severally show may be correlated with the various types of their prothalli. In fact, the embryogeny is to be interpreted in the light of these: and from this it will be seen again that a central type emerges. The embryo in all cases is *endoscopic*, that is, the apex is directed away from the archegonial neck. In all the species of *Lycopodium* in which the embryogeny is accurately known an early stage of the embryo is found in which it consists of a suspensor, defined by the first cleavage of the zygote; and of two tiers, each composed of four cells (Fig. 206). The first cleavages are variable in their succession, as is found to be the case also in other embryos; but their position shows considerable constancy. From the lower tier of cells, *i.e.*, that adjoining the suspensor, the foot arises, while the upper tier gives origin to all the other parts of the embryo. But after the first stages are past there is usually no sharp distinction

between the tissue composing the foot and that of the other parts: in the simplest cases it appears as though the foot were merely a region of tissue lying between the suspensor and the upper tier, rather than a definite organ, and it shares with the suspensor the office of maintaining connection with the prothallus. The type of *L. Selago* may be taken first, since it does not show any high degree of specialisation in its variable gametophyte, while it has been seen above that its mature sporophyte is one of the least differentiated in the genus. Its early embryogeny conforms to the usual type, as above stated (Fig. 207). The foot originates from the lower tier, and the various parts of the embryo from the upper; but the foot is only slightly developed. The upper tier of cells, limited below by the wall IV.-IV., soon assumes an unsymmetrical form, owing to the lateral upgrowth of the first leaf or cotyledon, while the apex of the axis originates early, near to its base: the relation of the apex to the intersection of the quadrant walls is a close one (Fig. 208, *A, B*). The axis soon proceeds to form successive

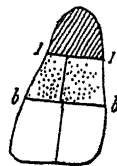


FIG. 206.

Diagram illustrating the primary segmentation of the zygote in *Lycopodium*. *l, l*=first segmentation wall which separates the suspensor, here cross-hatched. *b, b* separates a lower tier (foot-tier) here dotted, from an upper tier (stem-tier) left clear: each tier consists at first of four cells. The wall *b, b* corresponds to the wall IV.-IV. in Figs. 207, 208, 211, and to wall II.-II. in Fig. 210.

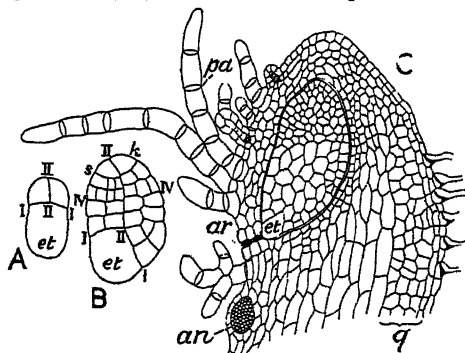


FIG. 207.

L. Selago. *A* and *B*, young stages of development of the embryo in longitudinal section. *et*=suspensor. *I*, the basal wall. *II*, the transverse wall, and *IV*, the wall dividing the shoot-tier from the foot: *s*=the apical side, *k*, the cotyledonary side. $\times 144$. *C*, median longitudinal section through a strong archegonial end of the thallus, which bears also an embryo; *an*, an antheridium; *ar*, archegonia and *pa*=paraphyses, all of which occupy the generative side of it, while rhizoids and the fungal region occupy the vegetative side. The enclosed embryo is orientated similarly to *B*, but it is older. $\times 57$. (After Bruchmann.)

leaves spirally arranged, and provided with chlorophyll. The tissue below becomes elongated as the hypocotyl, the length of which is determined by the level at which the prothallus lies in the soil (Fig. 209). The first root originates exogenously from the upper tier, just above the foot, and is succeeded by other roots of endogenous origin at higher points (Fig. 208, *B*).

Here, then, is an embryogeny characterised by its great directness and

simplicity. The only complication is the varying elongation of the hypocotyl according to the level of the prothallus in the soil; and there is good reason to think that this is an immediate adaptation to meet the varying levels of development of the gametophyte in the soil, in an embryo which is pertinaciously subaerial (Fig. 209). The nursing of the embryo by the prothallus is not long continued, nor is it structurally provided for, there being no de-

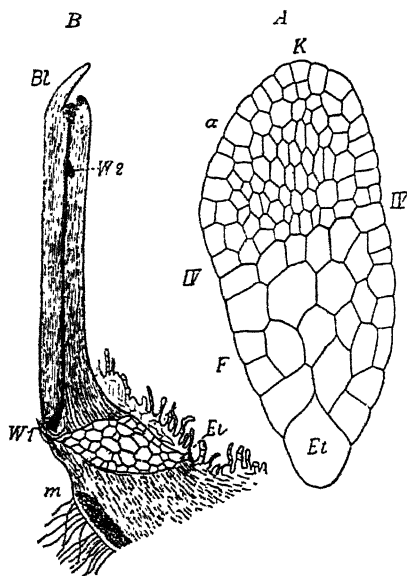


FIG. 208.

Lycopodium Selago. A = young embryo. $\times 150$. F = foot; IV-IV. = wall separating the foot from the stem-tier; K = cotyledon; a = apex; Et = suspensor. B = embryo more advanced, with prothallus still attached; BL = cotyledon; W₁, W₂ = young roots; Et = suspensor attached to the foot, which is clearly defined from the base of the axis. $\times 20$. (After Bruchmann.)

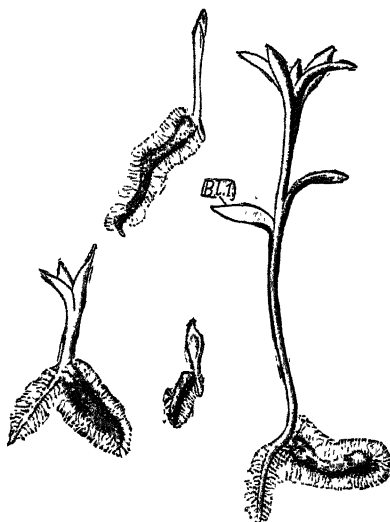


FIG. 209.

Prothalli of *Lycopodium Selago* with sporeling plants. $\times 3$. (After Bruchmann.)

velopment of an elaborate "calyptra," as in some other species; the embryo soon escapes from the prothallus, and fends for itself.¹

The type which corresponds most nearly to *L. Selago* is that of *L. Phlegmaria*, so accurately described by Treub.² Here the segmentation of the embryo, as well as the origin of all the parts and their proportions while young, have been fully made out. The hypocotyl elongates as the seedling develops, and the whole appearance of the sporeling resembles that of *L. Selago*. The primary segmentation in *L. Phlegmaria* is according to the scheme (Fig. 206), and the lower tier, as in *L. Selago*, forms only the foot, which attains no great size (Fig. 210, A, B). The upper tier develops unsym-

¹ This description is based upon Bruchmann, Gotha, 1908, and *Flora*, 1910. Some confusion has been caused by his naming the wall, II, in Figs. 206, 207, 211, the "basal wall"; whereas that term is usually reserved for the wall IV, IV.

² *Ann. Jard. Bot. de Buitenzorg*, vol. v., p. 87, etc.

metrically from the first, the side which will form the first leaf growing more strongly ; close to the base of the cotyledon, and apparently lateral owing to

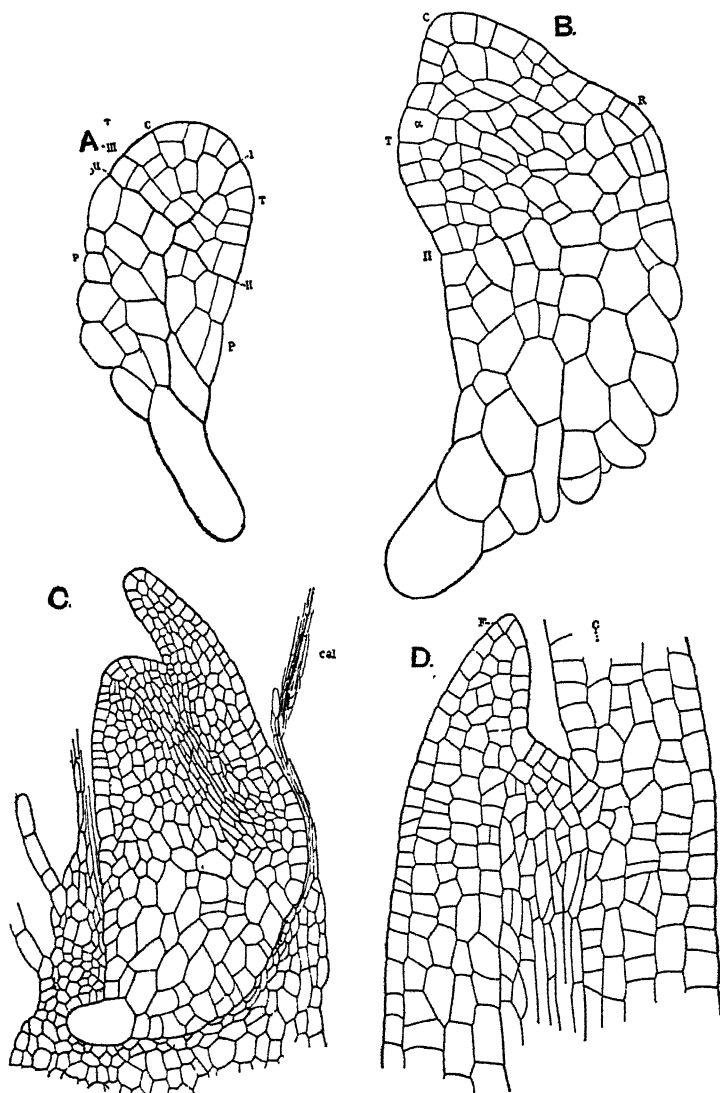


FIG. 210.

Embryos of *L. Phlegmaria*, in longitudinal section. *p*=foot; *c*=cotyledon; *T*=apex of axis. The wall marked *II* in *A* and *B* corresponds to the wall marked *IV* in Bruchmann's drawings (Fig. 207) and to the wall *b*, *b*, in Fig. 206. *C* and *D* represent older stages; in *D* the cotyledon (*c*) has been followed by a second leaf *F*, and the apex lies between them. *A* and *B* $\times 200$. *C* $\times 37$. *D* $\times 200$. (After Treub.)

the stronger growth of the latter but in reality terminal, arises the apex of the axis (*T*) ; it is, in fact, initiated in close proximity to the organic centre of the

upper tier. The root (R) also originates from the upper tier. A comparison of Treub's drawings of *L. Phlegmaria* with Bruchmann's series for *L. Selago* shows clearly the substantial similarity of the embryogeny in the two species, both of which are included in the sub-genus *Urostachya*. Both sporelings are from the first subaerial: their first leaves are green assimilating organs,

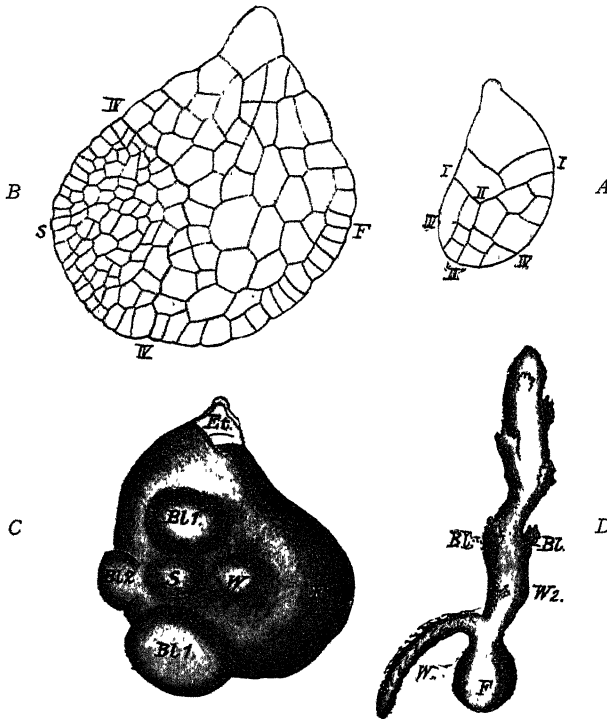


FIG. 211.

A=young embryo of *Lycopodium annotinum*. I.-I.=the basal wall; II.-II.=the transverse wall; IV.-IV.=the wall separating the foot-tier from the stem-tier. B=an older embryo of *L. clavatum*, showing more advanced development of the two tiers, and especially of the foot-tier. C=an older embryo detached, with cotyledons (BL1), a further leaf (BL2), and the first root (W), and foot (F). D=young underground, colourless sporeling; F=foot; W=root; W2=origin of a second root; BL=leaf-scales, of which the first pair are the cotyledons. A and B $\times 150$. C $\times 52$. D $\times 10$. (After Bruchmann, whose verbal description has been retained notwithstanding the confusion explained in footnote, p. 266.)

and differ in no essential degree from the normal foliage leaves. This may be held as a primitive condition.

But in the *clavatum-annotinum*-type the case is different. It has been seen that there the prothallus is developed underground, often at a considerable depth, and this brings with it modifications of the embryogeny. The first steps in the development are the same as in the types described above (Fig. 211, A); but very soon there is a conspicuous enlargement of the tissue of the foot, derived from the lower tier, adjoining the suspensor (Fig. 211, B):

a large spherical swelling is thus formed, which remains as an intra-prothallial haustorium (compare Fig. 201, *B*, with Fig. 211, *C*). The upper tier meanwhile progresses only slowly: two opposite leaves, one on either side of the stem-apex, appear late as compared with other species, their position relatively to the foot and to the suspensor not being constant (Fig. 210, *C*). The greatest development of the foot is not always in the plane of the median wall, but on

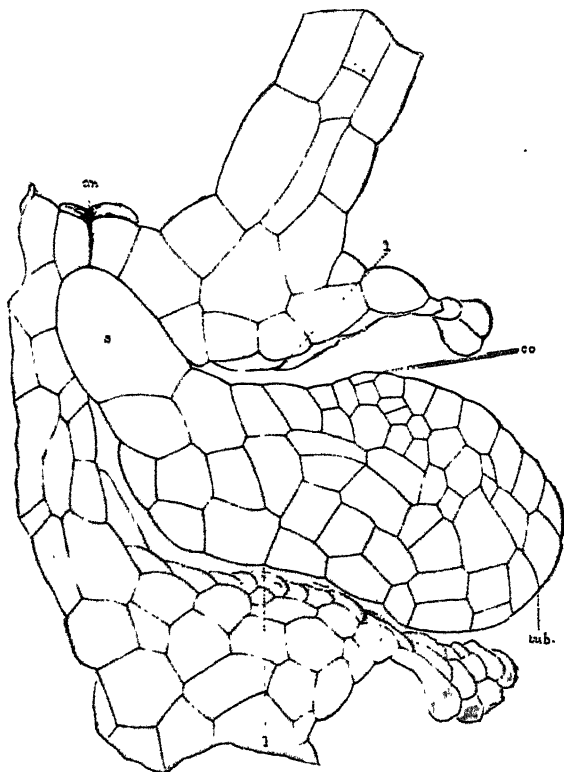


FIG. 212.

Lycopodium cernuum. Young embryo emerging from the prothallus. *ar*=neck of archegonium; *s*=suspensor; I-I. basal wall, corresponding to *b*, *b* in Fig. 206, to II-II. in Fig. 210, and to IV-IV. in Figs. 207 and 208; *co*=cotyledon; *tub*=tubercle of protocorm. $\times 300$. (After Treub.)

that side from which the greatest quantity of nutriment flows from the prothallus, and this brings about a torsion. The "foot" is here an opportunist growth, inconstant in position itself, and distorting in a variable manner the rest of the embryo. Soon after the origin of the first two leaves follows the origin of the first root, in a position variable relatively to them (Fig. 211, *C*). The embryo then bursts the tissue of the prothallus, as a consequence of active intercalary growth of the hypocotyl, which emerges upwards, while the root enters the soil downwards (Fig. 211, *D*). The axis while growing through the soil is pale, and bears only colourless scale-leaves, but on emerging

ultimately at the surface these pass into green leaves of the ordinary foliage type (Fig. 201, *A*). The embryogeny thus described is more complex than that of the *Selago*-type: its details are plainly in accordance with the saprophytic specialisation of the prothallus, and with its position deeply sunken in the soil. The embryo is long dependent for nourishment entirely upon the large prothallus; hence its swollen haustorial foot, which is developed most strongly in the direction of the largest nutritive supply, reacting meanwhile

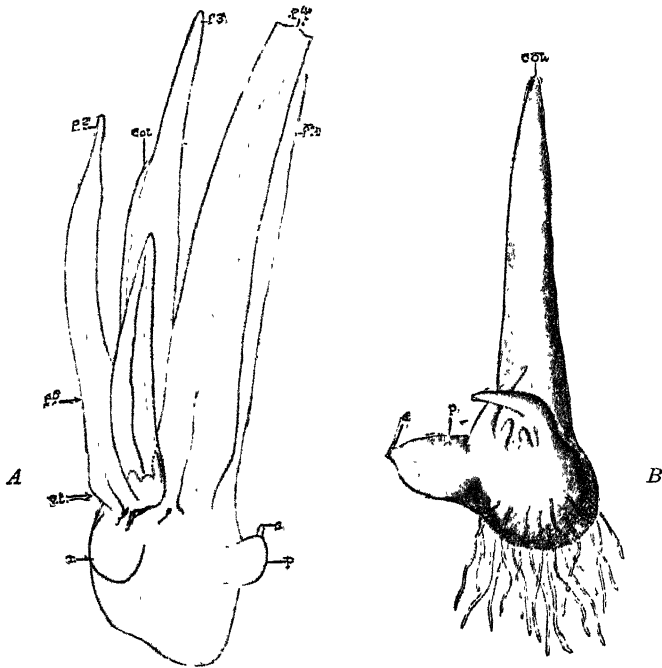


FIG. 213.

A and *B*, embryos of *Lycopodium cernuum*, showing protocorm. *s*=suspensor; *p*=foot; *col*=cotyledon; *f*¹, *f*², etc.=successive leaves; *r*=root; *vt*=punctum vegetationis. $\times 35$. (After Treub.)

upon the disposition of the other parts of the embryo: it results from unequal turgid distension and division of cells of the foot-tier, which in the *Selago*-type remain small. The first leaves are only scale-leaves, which may serve for protection of the apex in forcing its way upwards through the soil; but this is only a derivative function, and it can hardly be doubted, after comparison with the embryo of *L. Selago*, that the foliage character of the first leaves was the prototype, and that the early formation of colourless scale-leaves in the *clavatum-annotinum*-type is a concomitant of the subterranean habit adopted by their prothalli.

There remains the type of embryogeny of *L. cernuum* (Treub, *Buit. Ann.*, viii., p. 1), shared in all essentials by *L. inundatum* (Goebel, *Bot. Zeit.*,

1887, p. 183). Here the initial steps appear to be like those of other species, but the lower tier of cells which elsewhere forms the foot remains small, and as a body consisting of but few cells it serves to maintain a connection with the parent prothallus (Fig. 212). The upper tier originates the several parts of the embryo: breaking through the prothallial tissue it emerges early as a free-growing structure; but it soon swells into an undifferentiated tuberous body, the "protocorm," which is roughly spherical in form, composed exclusively of parenchyma, and attached to the soil by root-hairs. It is occupied by a symbiotic fungus. However similar to the swollen foot of the *clavatum*-type this "protocorm" may be, it is essentially a body of different origin: the foot springs from the lower tier of the embryo, and remains intra-prothallial: the protocorm originates from the upper tier, and is extra-prothallial. It was at first regarded as a foot which had quitted the prothallus; but developmentally it is distinct, while there is no evidence that an escape of



FIG. 214.

L. laterale. 66, young plant with fully developed protocorm and young stem-axis. $\times 4$. 67, young plant with branched protocorm and two stem-axes. $\times 4$. 68, 69, do. with young stem-axis and first root. 68×4 . 69×5 . (After Holloway.)

the foot from the prothallus ever took place. The part of the "protocorm" directed upwards bears a conical papilla of tissue, which develops into a cylindrical protophyll: this is a green assimilating organ, with or without vascular tissue: it is succeeded by other leaves of similar type, which are, however, indefinite both in number and in position (Fig. 213). Relatively late the apex of the axis may be recognised: it was probably defined from the first, but delayed in development. Its position is described as being near to the latest formed leaf, and the subsequent leaves arise from it in the usual acropetal succession, thus constituting the normal shoot. Close to its base the first root is also formed, and thus the normal plant is at length established.

More recently a "protocorm" has been observed in other species, particularly in *L. ramulosum* and *laterale* (Holloway, 1916, p. 227). It issues from the prothallus as a prone, seemingly amorphous body, capable of branching, and it bears protophylls on its upper surface without definite number or order. Those arising near to the base are small, and often lack any vascular supply. Sooner or later a stem-apex becomes apparent on the dorsal surface—or even more than one—surrounded by several protophylls, which gradually pass over in character to those of the leafy shoot (Fig. 214). The protocorm is green, and the protophylls bear stomata, while long rhizoids form attachment to the soil. The whole becomes detached from the prothallus after the

first protophylls are formed, thus appearing as an independent intermediate phase between the normal embryo and the definitive leafy shoot. Finally, a root is formed, the vascular strand of which connects with that of the shoot.

The existence of a tuberos stage as seen in species of *Lycopodium* gave rise to Treub's theory of the "Protocorm"; but before it is discussed the leading facts in the development of the sporophyte in *Phylloglossum* should be described. It has been seen that the prothallus is of the *cernuum*-type, and

that the embryo is attached laterally. Thomas (*Proc. R.S.*, vol. 69, p. 285) has found the embryo also to be similar to that of *L. cernuum*: it projects early from the prothallus, the cotyledon being the first part to emerge: this develops as an assimilating leaf, similar to those of subsequent years. A tuberos swelling is formed at once below the first leaf (Sampson, *Ann. of Bot.*, 1916, p. 606, Fig. A). Thomas states that no root appears during the first year's growth; but Sampson represents one. Clearly the facts require revision; but from the description of Thomas the embryology appears to be just that which might be expected of a plant which repeats in its annual cycle a development similar to, though not necessarily homologous in the strictest sense with, that of *L. cernuum*. The yearly growth of *Phylloglossum*

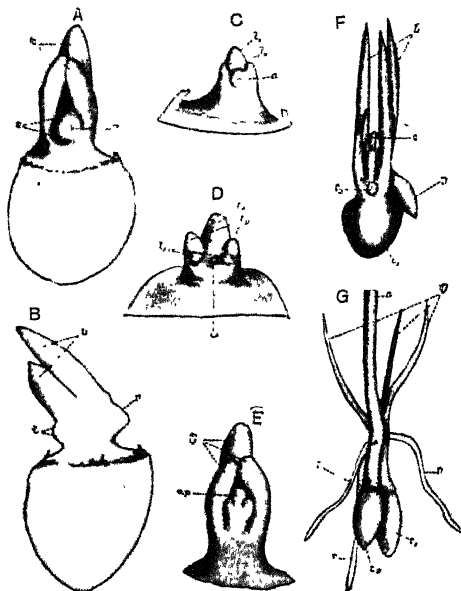


FIG. 215.

Phylloglossum Drummondii. A, B, frontal and side views of young plant which will not form a strobilus. C, D, similar plants, showing arrangement of the protophylls. E, a plant forming a strobilus. F, G, similar plants, older, showing mode of origin of new tuber; *t*=protophylls, *a*=apex; *t*=tuber; *r*=root. A-E $\times 14$. F $\times 3$. G $\times 2$.

resembles in many features that of the embryo (Bower, *Phil. Trans.*, 1885, p. 665, Plates 71-73): it originates at the apex of the storage-tuber formed during the preceding year, and its growing point retains its identity as the centre of the new growth. Sometimes only a single leaf is formed, but usually many—up to a dozen or more in strong plants: they arise in succession laterally round the apex, but are definite neither in number nor in position. They are of the same order of size and form as the embryonic protophylls of other Lycopods, though in strong plants of *Phylloglossum* they may be larger. Where the plant does not form a strobilus the apex, which lies centrally among the leaves, becomes depressed while the tissue surrounding it, continuing to grow actively but unequally, forms a process which develops into a new tuber (Fig. 215, A, B). Where a strobilus is formed it arises directly from the apex (C, D, E) and some

other provision has to be made for the formation of the new tuber. A growth then appears at the base of the peduncle bearing a central depression which is the apex of the new tuber: and this is carried outwards on an elongating process or "dropper," and invested by active intercalary growth (*F, G*). The dropper is tubular, owing to the deepening of the involution as the stalk elongates, and nutritive material is stored in its distal enlargement. The apex thus lies at the end of a deep channel which is finally closed by the surrounding cells. A slender strand connected with the vascular system of the main shoot traverses the stalk, spreading like a funnel below the apex of the tuber, but not continued into its distended storage tissue. The further development is the same whether the tuber is initiated from the original apex, or laterally where a strobilus is present.¹

The local relations of the tuber of *Phylloglossum* are like those of the extra-prothallial "protocorm" of *L. cernuum*. But in Treub's description of the latter the origin of the definitive apex of the axis was not brought into relation to the primary embryogeny: nor has its origin been clearly made out by subsequent writers. Observations carried out by Osborn in Australia throw a fresh light on the probable sequence of events where a new tuber is formed. Goebel had already shown how an old leaf of *L. inundatum* produced two tuberous adventitious buds resembling in form the sexually produced embryo (*Bot. Zeit.*, 1887, p. 186). Treub had also recorded adventitious buds in young plants of *L. Phlegmaria* (*Buit. Ann.*, vol. v., p. 127). The way was thus open for enquiry as to the behaviour of *Phylloglossum*. Osborn's results show not only that the plant as collected in the open is prone to adventitious budding, but also that this feature is related to its habitat, and can be produced experimentally (*Ann. of Bot.*, 1919, p. 485). He found that leaves, detached naturally or removed for purposes of experiment, produced, after more or less growth of a preliminary cell-mass, one or more tubers such as the plant normally forms in each season. Moreover, the stalk or dropper is as in the normal tuber. This demonstration of their adventitious origin confirms the view already expressed, that in fertile plants of *Phylloglossum* the new tuber is adventitious (Bower, 1885, p. 671). Thomas records the frequent occurrence of two new tubers on a single plant: sometimes on opposite sides of it, sometimes close together. Such facts seem to link the normal tuber-formation with that of the numerous buds observed by Osborn, borne on detached leaves; and they point to an adventitious origin in both cases.

The biological value of the tuber is evident in view of the severe climatic conditions under which *Phylloglossum* grows: they are those of alternating winter rainfall and prolonged summer desiccation. Like so many Australian plants it meets its difficulties by hypogean storage and rest. It is interesting to note, as Holloway does, that the three New Zealand species of Lycopods which are conspicuous in forming "protocorms," viz., *L. cernuum*, *ramulosum*, and *laterale*, all have green and leafy, though short-lived, prothalli, and all grow in localities that are subject to summer drought. But in *Phylloglossum*

¹ A feature described as "the organ of Mettenius" has frequently been noted by the earlier writers. It does not appear to be of constant occurrence, and probably it represents an enlarged adaxial lip of the depression which gives rise to the new tuber in fertile plants, rather than any more definite "organ."

it is the sporophyte also that is short-lived : excepting for its perennating tuber. In this it compares with *L. inundatum* ; here, however, the whole plant perishes in winter, excepting the distal bud. Such observations are important in relating the tuberous stage with seasonal stress.

What, then, is to be the place of the " protocorm " in comparative morphology ? Treub's theory, as based upon the embryos of certain Lycopods, was that it represents an ancient feature of phylogenetic importance : that certain young plants still form in the first instance not a rooted shoot but a rootless body (protocorm), bearing simple leaves (protophylls), and that this passes over later to the normal leafy shoot ; also that these events record a transitional phase between the embryo and the adult plant which figured historically in the establishment of the rooted sporophyte. In this relation the presence of a protocormous rhizome in the rootless plant of *Hornea* is an important positive fact, notwithstanding that other rootless Psilophytales are without it (see Chapter VII.). Thus a tuberous development was actually present in a class of very early vascular plants, though it was not a constant feature in the adult state of all of them : moreover, their embryology is still unknown. The inconstancy seen in the Devonian Psilophytales seems to match that in living Lycopods : and its occurrence may well have been then, as now, related to seasonal extremes. The adult *Hornea* would thus be comparable with the adult *Phylloglossum* in so far as its tuber is a recurrent feature. But, though this would accord with Treub's comparisons, it does not confirm his whole thesis ; in particular it does not indicate that a tuberous development, however useful in certain cases, has ever been an obligatory stage in the establishment of an independent vascular sporophyte. Tuberisation appears to be a secondary and sporadic rather than a general and primitive embryonic feature. This was the view stated in the *Land Flora* in 1908 (p. 355). *We may then agree with Von Goebel in the view that it will be best to drop the term " protocorm " with its atavistic implications, and recognise those swellings to which it has been applied as occasional adaptations, interpolated so as to meet a difficulty in establishing the young sporophyte under the stress of special conditions.* They are, from his point of view, arrested parts (Hemmungsbildungen) as regards anatomy, root-formation, and orthotropic growth (*l.c.*, p. 1120). Thus checked by external conditions in its normal development the tuber, partially or wholly hidden in the ground, collects reserve material to be used later in feeding the definitive shoot.

If the view of the tuberous development advanced above be adopted, the ground will be open for simple and direct comparison of the embryos of *Lycopodium* and *Phylloglossum* with a view to visualising a central and probably primitive type. The simplest embryogeny is that of *L. Selago* (Figs. 203, 204, 207, 208, 209) : here the embryo accommodates its growth in length to the level of its parent prothallus in the soil. Excepting for this it is of a constant type, without complications. The suspensor and foot are of moderate size, passing directly into the primitive shoot, which escapes early from the prothallus without any tuberous development and expands its first leaves as green photosynthetic organs. The apex of the axis is established early at the centre of the upper tier of cells. The first root is formed early

and is exogenous, as it is also in *Phylloglossum* (Bower, 1885, Figs. 34, 35). But it is soon followed by others that are endogenous. Thus the young plant is directly set up as an independent unit. The type most nearly corresponding to it is that of *L. Phlegmaria* (Fig. 210), and Bruchmann's later observations on *L. Selago* have strengthened the comparison (1910). In the *clavatum-annotinum*-type the primary embryogeny is the same; but the absorptive surface and storage-capacity of the embryo are enhanced by parenchymatous swelling of the intra-prothallial foot (Figs. 201, 211). The directness of this adaptation to the large saprophytic prothallus is indicated by the enlargement of the embryo being greatest on whatever side faces the greatest source of supply. The tardy development and late differentiation of parts accord with the longer nursing period, while the colourless scale leaves that appear earliest follow naturally, as in a potato, from the subterranean embryogeny. This is all fundamentally like what is seen in *L. Selago*, but secondarily modified in relation to the deeply subterranean mycorrhizic prothallus.

In the *cernuum-inundatum*-type the embryogeny opens as in other Lycopods; but the foot-tier remains small (Figs. 212-214). The origin of the cotyledon is as in *L. Selago*, but the extra-prothallial swelling in the upper tier profoundly disturbs the subsequent arrangements, so that detailed comparisons are difficult: in particular the origin of the axis is obscure. The type of leaf seen in the cotyledon is repeated in the protophylls, but without definiteness of position or number: their sequence is closed at last by the activity of the stem-apex, near to which the first root appears. Extreme examples are seen in *L. laterale* (Fig. 214). Here a rootless phase of morphological anomaly, initiated by extra-prothallial swelling in the upper tier, appears to have been intercalated in the regular embryogeny of the *Selago*-type. The swelling is related to the entry of a mycorrhizic fungus, but it may remain uncertain whether this is causal or a mere concomitant.

The *cernuum*-type is shared by *L. inundatum*, but not in an extreme form. It is this species which gives the nearest link with *Phylloglossum*, for its sporophyte perishes in winter, excepting the tip of the trailing stem which perennates. If such a condition were still further elaborated by the formation of an adventitious tuber in cases where the plant is fertile, or of a similar body as the product of direct apical growth where the plant of the previous year is sterile, the condition of *Phylloglossum* would be attained (Fig. 215). It would thus appear that *Phylloglossum*, so far from being a prototype of Lycopodinous development, is more probably a specialised offset from it. The characters which it repeats each year appear to be those of a secondary rather than of a primitive embryonic type. *And thus the embryogeny of the Eligulate Lycopods conforms to a single central scheme with variations upon it, which are no doubt biological betterments that meet special conditions. The type of L. Selago appears as the simplest, and it is probably also the most primitive of them all.*

PROTHALLUS AND EMBRYO OF THE LIGULATE LYCOPODIALES

The difficulty in germination of the Eligulate Lycopodiales has already been mentioned: its earliest stages, as recorded by De Bary and others, present no distinctive features; but they are liable to be held up till the fungal symbiosis is established in the free-living prothalli, which are monoeocious. In the Ligulate Lycopodiales, which are heterosporous, no such difficulty arises. Their dioecious prothalli are produced directly within the spores, and in both types of them the germination may begin before the spores are shed. Neither prothallus shows more than a small surface-exposure outside the ruptured wall. The microspore first partitions off a lenticular cell which, as it appears to perform no function and does not develop further, may be held as vestigial, representing the vegetative region

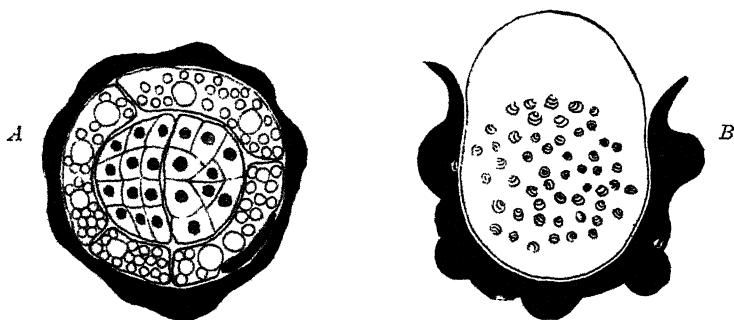


FIG. 216.

A. Microspore of *Selaginella apus*, after germination. (After Miss Lyon.)

B. Microspore of *Selaginella apus*, just before extrusion of the spermatozooids. (After Miss Lyon.)

of a male prothallus. The rest of the contents segment to form a wall composed of sterile cells surrounding a numerous group of spermatocytes (Fig. 216, A). The whole male prothallus thus consists of a unicellular vegetative region and an antheridium. When ripe a mucilaginous change appears in the walls of the cells: the outer coat ruptures on access of external water, and the biciliate sperms escape (Fig. 216, B, 217). The germination of the megaspore produces an internal tissue of greater extent, which is the female prothallus. Its development begins below the meeting of the three converging ridges of the tetrahedral spore, and it extends, by stages which vary in different species, into the spore-cavity with its store of nutritive material. Increase in bulk of the contents ruptures the wall along the three converging ridges, so that the surface of the prothallus is exposed (Fig. 217, IV). Near to the central point the first archegonium appears, while laterally others may be formed later, but not in regular succession. A vertical section through a germinated megaspore of *S. denticulata* shows it completely filled with tissue of the prothallus, while its exposed surface bears rhizoids (*rh*), some-

times borne on conical outgrowths, and archegonia in various stages of development (*ar*). The archegonium consists of a neck (*n*), composed of two tiers of four cells each; a canal-cell (*cc*), ventral-canal-cell (*v.cc*), and the ovum (*ov*); all of which are derived by segmentation from a single superficial cell of the prothallus (Fig. 217, v). When mature the neck is open, the canal-cell and ventral-canal-cell have disappeared, and the ovum is open to the access of the sperms. After fertilisation the zygote elongates in the axis of the archegonium, and segments rapidly to form a filamentous suspensor

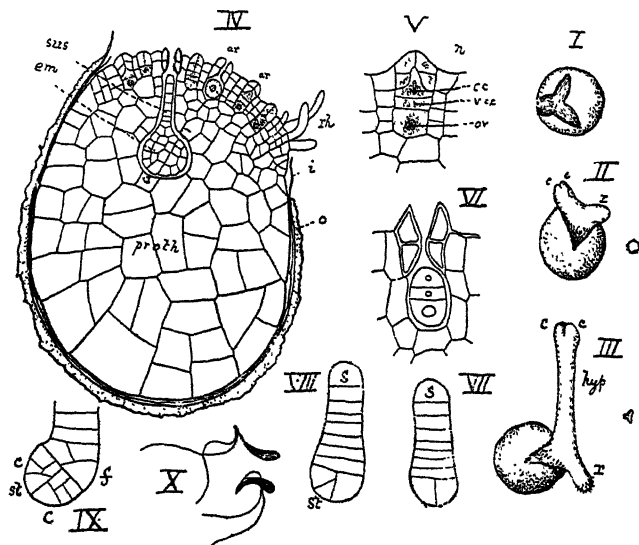


FIG. 217.

Embryology of *Selaginella dentisculata*, after Bruchmann. I-III ($\times 12\frac{1}{2}$) show germination of megaspore. IV, vertical section of megaspore showing prothallus, archegonia, and embryo (*em*) with suspensor (*sus*). $\times 50$. V, a mature archegonium. VI-IX, stages of developing embryo. X, spermatozooids of *S. cuspidata*, after Belajeff. $\times 250$.

(*s*), which thrusts the embryo deep down into the prothallus (Fig. 217, iv-viii). The distal cell soon enlarges, and divides. It gives rise centrally to the apex of the stem (*st*), with cotyledons right and left (*c*, *c*). Meanwhile unequal growth turns it to one side, and the convex side enlarges into the suckorial foot (*f*). Lastly, the first root (*wt*, Fig. 218) is initiated by periclinal divisions close to the attachment of the suspensor, and on the same side of the embryo. All the parts of the young embryo have thus been produced, while the apex, originally endoscopic, still occupies its distal position in the curved embryo. As the axis and root grow they protrude from the ruptured spore, the root turning downwards and the elongating hypocotyl upwards (Fig. 217, iii, *hyp*). The cotyledons already bear ligules (*l*, Fig. 218). A young *Selaginella* plant is thus established with parts similar to those of the parent.

The details thus briefly described, and shown in Figs. 217, 218, relate to *Selaginella denticulata* as observed by Bruchmann (*Flora*, Bd. 104, 1912, p. 192): this is a small and dorsiventral, but not highly specialised, species, and it may be taken as a middle example.

It has been already pointed out that *Selaginella spinulosa* may be held to be more primitive as regards the morphology of the mature plant than the dorsiventral species of the genus; and further, it has been seen that it differs from them anatomically, showing a vascular structure which is probably more primitive also. This gives a special interest to its embryology, which has been fully worked out by Bruchmann (*Unters. ueber "Selaginella spinulosa,"* Gotha, 1897). The early stages are essentially as in *Lycopodium*,

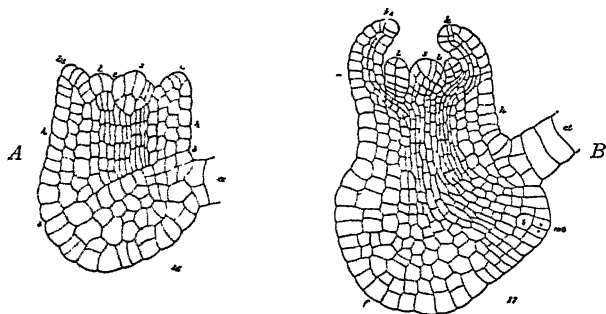


FIG. 218.

Embryos of *S. denticulata*, after Bruchmann. *et*, suspensor; *wt*, root; *f*, foot; *b*, *b*, basal wall; *h*, hypocotyl; *s*, apex; *k*, *k*₁, cotyledons; *l*, ligule.

resulting in a suspensor, and two tiers of four cells each, forming the embryo: the whole structure is at first straight, with the apex flattened (Fig. 219, *A*, *B*). The suspensor thrusts the embryo downwards into the tissue of the prothallus. The lower tier of cells of the embryo (*i.e.*, that between walls 1., 1. and 1v., 1v. in Fig. 219, *A* and *C*) contributes to the hypocotyl, which may here be greatly elongated and curved: it becomes thus a prominent feature of the embryo. At its base, in close relation to the suspensor, the first root arises in a lateral position. The products of the upper tier at first remain small (*i.e.*, above wall 1v., 1v., Fig. 219, *A*, *C*): the formation of the first cotyledon may be long delayed, sometimes it may still be wanting even when the axis has already curved obliquely to the suspensor. The second cotyledon may be even longer delayed: in some cases it only appears after the shoot issues from the spore. Thus sooner or later two opposite but unequal cotyledons successively make their appearance. The apex of the axis, which has no single initial cell, lies between them, originating from the centre of the flattened apex of the embryo (Fig. 219, *A*, *B*, *D*). As the hypocotyl elongates the embryo curves so that the axis takes a vertical position, while the suspensor is pushed to one side by the growing root. Finally, the shoot emerges above ground, and the two coty-

ledons developing at last to equal size appear as assimilating leaves (Fig. 219, *G*, *H*). According to Bruchmann no enlarged foot is formed in this species, and the same appears to be the case in *Selaginella apus*. Comparing this embryogeny with that so well known in *S. Martensii*, there is essential

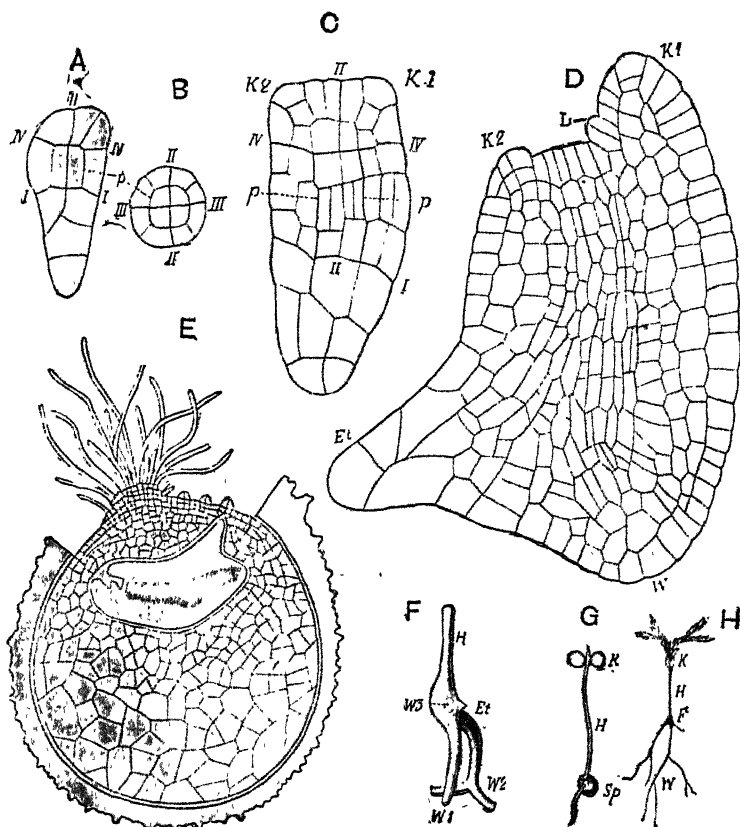


FIG. 219.

Embryos of *Selaginella spinulosa*. *A-D* illustrate the segmentation. *I*, *I*, first wall, separating the suspensor; *IV*, *IV*, corresponds to wall similarly marked in Figs. 207, 211; and to wall *b*, *b* in Fig. 206; *p*=wall marking off the vascular strand of the axis; *K*, *K*=cotyledons; *L*=ligule; *W*=root. *E*=section of germinated spore with embryo *in situ*. *G*, *H*=seedlings. *H*, natural size; *G*, enlarged. *F*=the basal knot enlarged; *Et*=suspensor; *W*₁, *W*₂=roots. (After Bruchmann.)

similarity in the disposition of the parts. The chief differences lie in the presence of an haustorial swelling of the hypocotyl in the latter species, and in the fact that in it single initials are found at the apices of stem and root.

Bruchmann's researches have disclosed some latitude in the detail of development among the species of *Selaginella*. This affects the apical segmentation; the equality or inequality of the cotyledons; the presence or absence of a distended foot; and the relation of the first root to the other parts.

Fig. 220, *a*, *b*, *c*, represents in outline and cellular construction three types of embryogeny in *Selaginella*. They are so orientated that the shoot points upwards, and the same parts are involved in each. In *a* the first root is on the same side as the suspensor; but in *b* it is on the side opposed to it; in *c* it is on the same side as the suspensor, but it lies between the suspensor and the apical bud, and in close juxtaposition with the former. Thus the root is variable in position relatively to the other parts. But the final result as regards the form of the sporeling is substantially similar for them all;

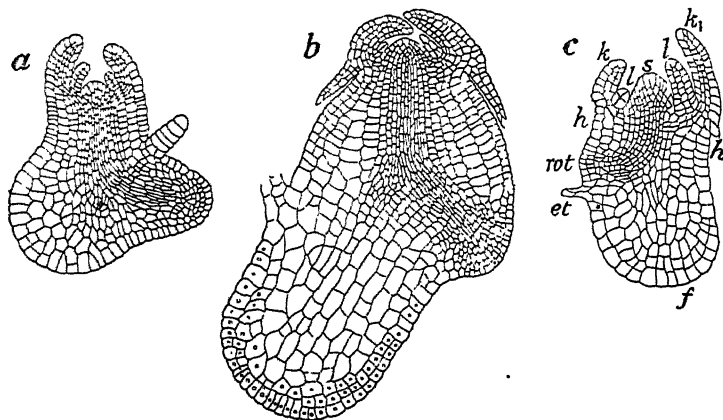


FIG. 220.

Embryos of *Selaginella* orientated so that their apices shall point upwards, and demonstrating the variability of position of the first root. (After Bruchmann.) *a* = *S. denticulata*, the suspensor pointing obliquely upwards, and root on the same side as the suspensor, but remote from the apex. $\times 150$. *b* = *S. Poulteri*, with suspensor pointing obliquely upwards, but the root on the side opposite to it. $\times 100$. *c* = *S. Galeottii*, suspensor horizontal, root on same side as suspensor, but between it and the apex. $\times 150$.

examples are shown in Fig. 221, *a-d*, where the older sporelings of various species are orientated as they would be in nature.

Comparing the embryogeny of *Selaginella* with that of *Lycopodium*, it seems remarkable that the similarity should be so great as it is when the difference between the parent prothalli is so marked; we are thus comparing an embryo produced by a free-growing, bisexual prothallus in *Lycopodium* with that of an endosporic, unisexual, storage prothallus in *Selaginella*. In either case there is a pluricellular suspensor and two tiers of cells of the embryo. In the later development the nearest similarity is between *L. Selago* and *S. spinulosa*: in both there is a marked elongation of the hypocotyl, with the first root originating laterally near to its base; there is the same absence of any determinate foot, and as a rule the same origin of a first cotyledon laterally, with the apex of the axis between it and the next-formed leaf. In both the axis originates in close relation to the intersection of the primary segmentation-walls of the upper tier of the embryo. The position of the first root relatively to the other parts is also alike in *L. Selago* and

S. spinulosa: the similarity of the embryogeny of the genus *Selaginella* to that of *Lycopodium* is thus most marked in two species both of which are held to be primitive in their respective genera, as judged by comparison of the adult sporophyte. Finally, in neither of them is there any extra-prothallial swelling of "protocormous" nature; but in *S. spinulosa* there is that basal knot or swelling at the foot of the hypocotyl which has already been mentioned in Chapter XI. (Figs. 155, 156, pp. 208, 209). Whatever its real nature may be it is the source from which the subsequent roots arise. This office it shares with the rhizophores of other species of *Selaginella*, and with the Stigmarian trunks of the dendroid fossils (Fig. 221).

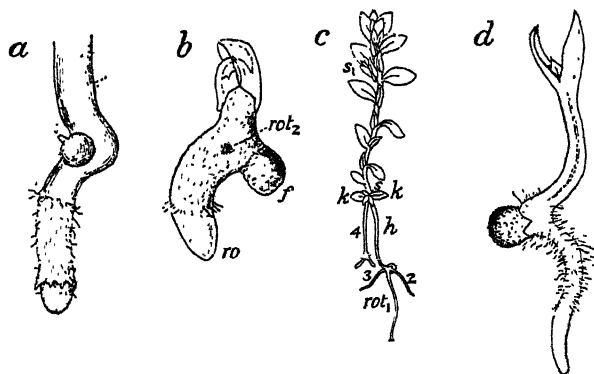


FIG. 221.

Sporelings of *Selaginella* orientated in their probable living positions. *a* = *S. Martensii*, showing the upward hypocotyl, and downward first root breaking through the "rhizophore"; to the left the suspensor pointing obliquely upwards; below it the second "rhizophore." The foot is very slightly developed. $\times 32$. *b* = *S. Gabelii*, with the same relative position of parts, but the suspensor is not seen, and the foot is better developed. $\times 32$. *c* = *S. Gabelii*, a more advanced plant, with successive rhizophores (1-4); *h* = hypocotyl; *k, k*, cotyledons, *s, s*, dormant buds. $\times 3$. *d* = *S. Kraussiana*. (After Campbell.) $\times 12$. *a, b, c*, after Bruchmann.

Examples of apogamy in *Selaginella* have been reported by Bruchmann (*Flora*, 1912, p. 212) in *S. rubricaulis* and *spinosa*, and by Von Goebel in *S. anocardia* (*Flora*, 1915, p. 324). In these species the microsporangia are few, or absent. The megaspores of *S. rubricaulis* were collected by Bruchmann from sprays bearing only megasporangia. The result of their germination was that sporelings were produced, though detailed observation showed that the archegonia had not opened. Von Goebel sowed the megaspores of *S. anocardia* in the absence of the very rare microspores, and obtained similar results. He suggests, by analogy with other cases of apogamy, that the megaspores were produced without meiosis, and were themselves diploid: but cytological examination of their development was not recorded. From the facts it would not be justifiable to say that the apogamy is a consequence of the absence of microspores; but rather that the same cause (absence of reduction) may probably account both for their rarity or absence, and for the apogamous production of embryos. (Compare the case of *Marsilia Drummondii*, Strasburger, *Flora*, 1907, p. 123.)

The germination of the spores of *Isoetes* is in all essential points like that of *Selaginella*. The female prothallus fills the whole of the megaspore with a uniform tissue, and the first archegonium lies at its apex, at the point of convergence of the three fissures of the spore-wall. There is no basal cell;

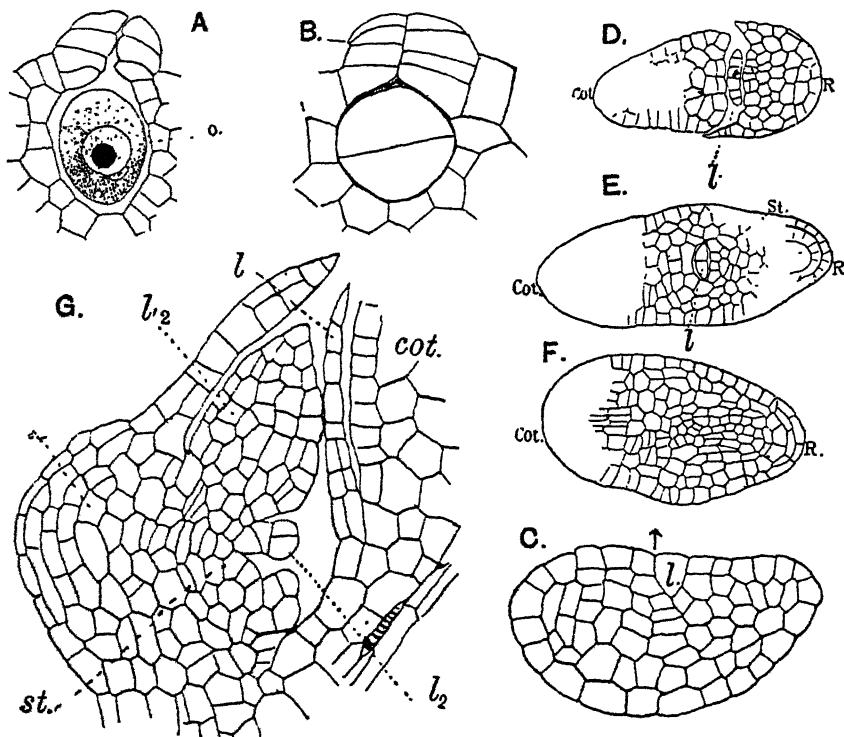


FIG. 222.

Isoetes echinospora, var. *Braunii*, Dur. $\times 365$. A=an archegonium. B=a two-celled embryo within the archegonium. D, E, F=three successive horizontal sections of a somewhat advanced embryo; R=root; cot=cotyledon; st=stem; l=ligule. $\times 175$. C=median longitudinal section of a young embryo; l=ligule. $\times 200$. G=median section of a young sporophyte with second leaf, l₂, already formed; l₂=ligule of second leaf; r₂=second root; st=stem apex. $\times 150$. (After Campbell.)

the neck is sunk in the thallus, and consists of four tiers of four cells each: there is a single canal-cell, ventral-canal-cell, and ovum.

At first sight the embryogeny of *Isoetes* seems to differ radically from that of *Selaginella*, notwithstanding that the endosporic prothallus is so similar. The key to the difference is first the inversion of the exoscopic embryo, as compared with *Selaginella*; and secondly, the entire absence of any suspensor: what remains in *Isoetes* may be held to correspond to the product of the two upper embryonic tiers only. The first division of the zygote is by a wall more or less inclined to the axis of the archegonium (Fig. 222, B): this indeterminate position of the "basal wall" is theoretically important, as

bearing on the inversion of the embryo in the archegonium as compared with that in *Lycopodium* or *Selaginella*. The two tiers thus initiated are usually called the hypobasal and the epibasal; but the octant divisions commonly seen in other embryos are not always clearly defined in *Isoetes*. The hypobasal tier here forms the foot only: all the other parts originate from the epibasal tier; the cotyledon with its ligule is the first part to be organised; it is followed soon by the first root, which arises at the opposite side of the epibasal tier to the cotyledon (Fig. 222, *C, D, E, F*). Between these parts a slight depression is formed, and it is surrounded by a semicircular ridge: within this the apex of the axis is at last organised, and it soon gives rise to the second leaf, which faces the cotyledon: the very exiguous apical cone (*st*) lies between them (Fig. 222, *G*). And so the shoot is established, bearing successive leaves with spiral arrangement, and successive roots, of which the second is below the base of the second leaf.

Comparing this apparently divergent embryogeny with that of the Lycopods above described, if the whole embryo be imagined inverted in its orientation relative to the archegonial neck, and their suspensor be imagined entirely away, then the two embryonic tiers may be compared with those seen in *Isoetes*. Here, as in *L. Selago* and *L. Phlegmaria*, the hypobasal tier forms the suctorial organ only, and takes no direct part in the establishment of the plant. The epibasal tier is like that of *L. Selago* as regards the parts which it initiates and in the positions which they severally hold; but differs in its growth in length being stunted, and in the early ascendancy of the cotyledon, which condition it shares, however, in some measure with *L. Phlegmaria*: it differs also in the late definition of the apex. But the position of the latter relatively to the whole embryo is the same, for the stem originates in close relation to the centre of the upper tier of the embryo, as it does in all the Lycopods where the embryogeny has been exactly followed. The apical cone is small in bulk and late in appearance, these being probably correlative consequences of the early advance of the cotyledon, and accentuated by the stunted state of the adult stem. It is thus possible to see even in the embryo of *Isoetes* some clear relation to the plan which, with such curious modifications, underlies the embryogeny of the Lycopods. This relation has been strengthened by the statement of La Motte (*American Journ. of Bot.*, vol. 20, p. 217, 1933), that the embryo of *Isoetes* shifts its position as it grows, until its long axis lies roughly parallel to the apical surface of the gametophyte. This change of orientation is interesting for comparison with the curvatures of adjustment seen in the embryos of *Selaginella*. But the comparison cannot be fully established till the facts are related to the direction of gravity during the development of the embryo (compare Figs. 220, 221).

In view of the delicacy of the tissues composing the prothallus of the homosporous Pteridophytes, it could hardly be expected that they would be preserved as fossils. Nor would it be probable that the germinated micro-

spores of heterosporous types should be found. But sufficient is known of the female prothalli, preserved either within or in close relation to the indurated megaspores, to show that in Lepidodendroid fossils their general features were like those of *Isoetes* or *Selaginella*. A good example has been seen within the megaspore of *Lepidostrobus Veltheimianus*, where a delicate prothallus fills the cavity of the spore; while opposite the open beak of the megaspore a reasonably preserved archegonium has been seen, with deeply sunk venter and a slightly projecting neck.¹ The analogy with *Selaginella* is plain. Perhaps the most striking example is that figured by McLean from the Lower Coal Measures, and referred on account of the appendages on the thick wall of the spore to *Bothrodendron*. Here the spore had ruptured, and the prothallus is seen to project in irregular lobes, as in *Selaginella*. There are indications of several sunken archegonia, but unfortunately none of them has been cut in a median plane (Fig. 223).² In these instances the spore

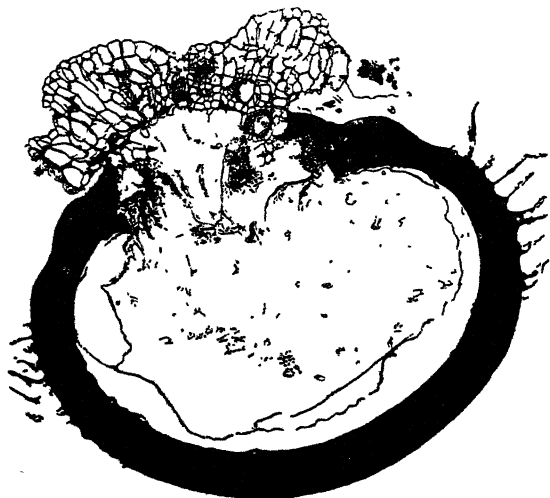


FIG. 223.

Germinated megaspore of *Bothrodendron* (After McLean.) Seen in median section. The prothallus projects and embedded in its parenchyma large cavities are seen to the right, believed to be archegonia. Probably the section has traversed them obliquely, and their necks are not seen.

has been shed, as in *Selaginella* or *Isoetes*; but where the spore is retained within the sporangium, as in *Lepidocarpon* and *Miadesmia*—or shed after fragmentation, with parts of the sporangium still attached, as in *Mazocarpon*—the prothallus has been found filling the spore-cavity; here, however, the archegonia have not been well seen.³ Provisionally such evidence may be held as sufficient to show that in the Lepidodendroid fossils the female prothalli were of the same general type as those of *Selaginella* and *Isoetes*.

¹ Scott, *Studies*, Figs. 81, 83.

² *New Phyt.*, vol. xi., 1912, p. 311.

³ Scott, *Studies*, Fig. 82, after Dr. Benson.

CHAPTER XV

LYCOPODIALES

SUMMARY AND CONCLUSION

IN Chapters XI-XIV the Lycopodiales have been examined from the various points of view of habit, anatomy, the spore-bearing parts, the gametophyte, and embryology. Such wide comparisons have led to the recognition of generalised fundamental types of the Lycopods from which divergent lines of specialisation may be traced within the Class. A fact that cannot fail to carry weight is that, though the Eligulate or the Ligulate Series stand consistently apart in the feature that their names connote, they respectively diverged from certain types among plants still living, which may be held as being themselves relatively primitive. Among the Eligulatae such a living type is suggested by *Lycopodium Selago*, and by *Selaginella spinosa* among the Ligulatae. These, notwithstanding the ligular difference between them, resemble one another in such various features as the radial conformation of the sporophyte, the relatively primitive vascular tracts, the sporangial characters, and the embryogeny. This correspondence in respect of leading features, whatever its phyletic meaning may be, suggests that the two branches of their Class are naturally allied, and that the Lycopodiales are all really akin. The central feature confirming this is their common type of sporangium, together with the constant relation of a single sporangium to a subtending leaf.

Conversely, if we take such central types as starting points, we may trace outwards from them probable lines of specialisation in the Class. The results ultimately reached may appear widely divergent, but commonly the differences can be recognised as adaptations to external conditions of life, and examples may be drawn either from the Lycopods living to-day, or from related fossil forms now extinct. This aspect of the Lycopodiales, however imperfectly traced, will indicate in broad lines the track of evolutionary progress within the Class. Its consequence may be the presentation of central types still living as those best fitted to raise the question of evolutionary origin of the very coherent Lycopod-type.

The habit of the sporophyte in those relatively primitive species of *Lycopodium* which constitute the *Selago*-section of the genus is characterised by a radial shoot with dominant axis, undifferentiated leaves, and dichotomous branching ; in some of the mountain species there may be but three or

two, or even only one forking—a simple structure which points to the possibility of an originally unbranched shoot. The plant is decumbent below, and is attached to the soil by dichotomising roots. Fig. 148 suggests the habit in a specimen of *L. Selago*, which grew to unusual height among heather on a Scottish hill. The first leaves in this species are green and sterile; but sporangia have been observed by Bruchmann as appearing after the second branching of the young axis. This is early as compared with most species, but in large Andean species, such as *L. Trencilla* and *firmum*, they have been observed in the leaf-axils down to the base of the adult stem. Thus practically the whole plant is here a strobilus, excepting the first leaves, a state which was probably primitive for the class. The *Selago*-group illustrate a differentiation in such a continuous strobilus, which may be referred to abortion of the sporangia in certain zones. In Fig. 148 such sterile zones are seen to alternate with fertile zones, but without differentiation of the leaves by size or form; moreover, imperfectly formed sporangia are habitually found at the limits of those fertile zones, which probably mark seasonal periods of fertility. Such facts indicate a progressive sterilisation of a uniformly fertile shoot, leading towards a segregation of sterile and fertile tracts. This state has been described as the *Selago*-condition.

In the Ligulate Series a parallel may be found in *Pleuromeia* and *Isoetes*. In either of these the unbranched axis is sooner or later fertile. In the former the sporophylls are disposed in a distal cone. In *Isoetes* all the adult leaves appear to be potential sporophylls, as shown either by actual sporangia borne upon them, or by various degrees of their imperfect development, and these are associated together irregularly, though the form of the leaf does not vary. In fact *Isoetes* shows the *Selago*-condition. A similar state has been seen to exist in *Pinakodendron*, a large fossil from the Coal Measures allied to *Bothrodendron* (Scott, *l.c.*, p. 183). In some Selaginellas early fertility has been seen; for instance, Bruchmann has shown that in *S. Preissiana* the stem of the sporeling forks above the two cotyledons: while one limb is arrested the other may grow directly into a fertile cone, with only a score or so of sterile leaves between the cotyledons and the sporophylls. But in most species fertility appears only later, while the strobili are clearly marked off from the sterile region. All this suggests that in the Lycopods, whether Eligulate or Ligulate, the whole shoot was once potentially fertile after the first stages had been passed.

From such a starting point various lines of elaboration of the sporophyte may be traced, and they are often open to ready biological explanation; moreover, they appear to have run in some degree parallel in the Eligulate and the Ligulate Series. First, progressive sterilisation by abortion of sporangia increases the vegetative region: this has led to more definite specialisation of the part that remains fertile, which is usually distal. Here the sporophylls tend to develop as protective rather than as nutritive organs.

They are, however, in varying degree provided with stomata, and thus they aid the ventilation of the tissues of the propagative region. By such steps the fertile strobilus becomes a compact body clearly marked off from the photosynthetic shoot. Once distinct from the propagative strobilus the vegetative region was susceptible of further specialisation. In the dendroid fossils, and in some large Lycopods and Selaginellas, it attained large size before bearing cones. As a rule it retained its radial symmetry, though in smaller forms a straggling or climbing habit has led sometimes to dorsiventral development, which is occasionally extended to the more conservative strobilus itself; but this usually retains its radial symmetry. Even extreme types, such as the larger species of *Lycopodium* and *Selaginella*, *Lepidodendron*, *Sigillaria*, *Pleuromeia*, *Isoetes*, and *Phylloglossum*, are thus referable back in origin to a less differentiated fertile shoot, originally perhaps unbranched. The *Selago*-type lies near to the source of these elaborations, and links them all together.

Advances in form and in size in the Lycopods are seen to be accompanied by increasing complexity of the conducting tracts; but in all of them the more advanced structure is referable in origin to the non-medullated monostele, from which the adult state advances in the individual life. The ontogenetic changes have been described for certain examples in Chapter XII: a brief summary will therefore suffice. In the adult shoot the stele appears to be cauline, and the leaf-traces mere appendages upon it, though this analysis appears difficult of application sometimes in the sporeling, as well as at the distal end of the strobilus. Notwithstanding their size certain of the Ligate fossils have retained the solid cylindrical core of purely tracheidal wood with great persistence, merely enlarging it to meet the increasing demand. But where the size is great medullation and crenulation may appear: while often cambial thickening has produced a secondary zone, as in many of the fossils (Figs. 175, 176). These tree-like forms have all died out, leaving only the modern *Isoetes* as a pale reflection, structurally condensed and confused, of their gallant attempt to make the best of a deficient plan. On the other hand, the living genera *Lycopodium* and *Selaginella*, with their numerous species, have achieved a certain degree of success by elaborating the non-medullated monostele without cambial thickening. The former has exploited this simple type to the full along conservative lines, but with the important modification of encroachment of phloem and living parenchyma into the dead woody core, thus converting it into a vitalised xylem-sponge: a concession which seems to have met the demand even in the largest of these somewhat stunted Club Mosses (Figs. 168, 169). The radial type of *Selaginella spinosa* presents a stelar structure like that of a small *Lycopodium* (Fig. 173). But in the dorsiventral species of *Selaginella* the conducting tracts reflect their own symmetry in the flattened monostele, which becomes folded, and ultimately polystelic in the largest of them (Fig. 171). In the

rhizome of *S. Lyallii* a solenostelic structure appears, sometimes with two concentric rings, as in certain polycyclic Ferns. On the other hand, its upright aerial stems contain many meristeles, as in the advanced Leptosporangiates (Figs. 172, 173). All of these structural departures from the primitive monostele may be regarded as means of adjusting surface to bulk of the dead wood as the size increases. Morphologically they are all referable back in origin to the non-medullated monostele, which is seen in the young plants. In *L. Selago* this simple structure is but little modified in the adult, an anatomical fact that indicates its primitive state (compare Fig. 169, C).

The sporangia of the Lycopodiales all conform to one general fan-shaped type, and there is a singular constancy in their position relatively to the subtending sporophylls; with very rare exceptions (amounting even to abnormality) one sporangium shares its median plane with its sporophyll (Chapter XI). But the form and dimensions of the sporangia vary in detail. In the non-specialised *Selago*-type the sporangium is stalked, narrowly fan-like, and radially compressed, the archesporial cells forming a single tangential row (Figs. 182, 183). In the *clavatum-alpinum*-type they are more broadly sessile, with three tangential rows of archesporial cells, in certain proved examples, and a more fan-like spread. This appears to go along with a more definite strobilus, and more detailed sporangial protection (Figs. 185, 186). The interest in these differences in the Eligulate Series lies in the fact that they help to explain what may be seen as a more prominent feature among the Ligulatae. For here the sporangium may be radially elongated in much higher degree, giving a greatly enhanced spore-output. For instance, in *Isoetes* the number of tangential rows of archesporial cells is higher than in any observed species of *Lycopodium*, leading to the broad cake-like adult state (Fig. 155). Such radial extension of the sporangium is seen in an extreme form in the large cones of *Lepidosirobus* (Figs. 195, 196). An interesting point in these large sporangia is the partial sterilisation of the sporogenous tissue to form trabeculae, which are probably effective in meeting mechanical and nutritive demands. This leads towards a condition of septation, and instances are seen in *Cantheliophorus*, and in the megasporangia of *Mazocarpon*, which may best be so interpreted. The heterosporous state was probably assumed after the general character of the Lycopod-sporangium had been defined, and it does not appear to have materially affected the morphology of the shoots where it occurs, however great the effect may be upon the prothalli and embryos which follow.

Comparison of Lycopod sporangia thus leads back from such specialised types as those last described to a homosporous, stalked and radially compressed body; and each of these was habitually associated with a subtending sporophyll. The *Selago*-type or that of *Selaginella spinosa* may be held as relatively primitive examples.

The various types of prothalli of *Lycopodium* appear at first sight to be

widely divergent, a result consequent on their differences of habit and nutrition—whether exposed and photosynthetic, buried and mycorrhizic, or saprophytic in the bark of trees. The descriptions given in Chapter XIV indicate that initially the common form of the prothallus is that of an inverted cone, starting upwards from the spore or from the gemma, but with sluggish distal growth. In the *cernuum*-type the lower part of the cone is buried in the soil, and is fungus-infected; the upward-directed crown, which is photosynthetic, may bear irregular leaf-like lobes, the sexual organs being seated about their base (Fig. 200). In the wholly underground *clavatum*-type the correlative of the basal region of *L. cernuum* develops as a widely expanded cone, irregularly cup-shaped but without leaf-lobes; the sexual organs are borne upon the flattened crown, as in *L. cernuum* (Fig. 201). In the *Phlegmaria*-type (Fig. 202) the apical growth and branching are more pronounced, and the saprophytic prothallus is strap-shaped, and spreads widely, though its conical origin is readily seen on germination of the gemmae. The thallus of the *Selago*-type takes a middle position both in form and in habit. It has an obconical form, and is mycorrhizic below. Sometimes it is green when it rises above ground, but it is without leaf-lobes, and is exceptional in showing a slight tendency to dorsiventral development of the lip of the narrow cup; the sexual organs are similarly placed to those of *cernuum* and *clavatum* (Figs. 204, 205). These features, together with the level of the development at or near to the surface of the soil, confirm the suggestion that the prothallus of *Lycopodium Selago* is, like its sporophyte, a central and relatively primitive type.

The known Ligulatae are all heterosporous, and the effect of this is so far to modify the prothallus that comparisons of its form, of the same nature as those among the Eligulatae, would be of little value.

In the initiation of the embryo all Lycopods in which it has been followed—except *Isoetes*—conform to one type, but this is subject to variations of form as the development proceeds. The polarity is stamped by the first cleavage of the zygote, which is by a wall in a plane transverse to the axis of the archegonium. The cell directed towards the neck forms the suspensor, the other may be called the embryonic cell, and it forms the several parts of the sporeling. Thus the embryology is *endoscopic*. In *Lycopodium* the embryonic cell then divides into octants by walls at right angles to one another (Fig. 207, *A, B*; 211, *A, B*). The succession of appearance of the cleavages is not uniform, but the constant result is that the embryo is constituted of two tiers of cells separated along a line marked *rv*. in the Figs. quoted, which is here described as the *basal wall*: the tiers are then respectively epibasal and hypobasal. Lateral outgrowths in the epibasal region, first on one side and later on the other, give rise to the two cotyledons, between which, that is, at the centre of the epibasal region, the apex of the stem appears. The first root originates exogenously from the lower

part of the upper tier, while the lower tier forms the foot by which physiological connection with the prothallus is maintained. The embryo with its parts thus laid down may undergo a varied further development.

In *Lycopodium Selago* the whole embryo elongates, but especially in the region above the root forming the hypocotyl. In this species there is no special enlargement either of the intra-prothallial foot, or of an extra-prothallial tuber. It appears spindle-shaped as the simplest form of Lycopod embryo. But in many other species tuberous growths appear early, and are apt to distort the embryo. In the *clavatum*-type there is an enlarged intra-prothallial foot, serving an haustorial function in drawing nourishment from the large mycorrhizic prothallus till the photosynthetic shoot appears above ground (Figs. 201, 211). In the *cernuum*-type, and in *Phylloglossum*, an extra-prothallial swelling appears as the "protocorm" or tuber (Figs. 212, 213, 215). In extreme cases this may interpose a substantive but amorphous interlude between the embryo and the leafy plant (Fig. 214). The nature of these swellings has been discussed in Chapter XIV. All such developments, which distort the simpler type of *L. Selago*, are probably of the nature of special biological adaptations, rather than inherent features of the embryological history.

The embryo of *Selaginella spinulosa* bears a close resemblance to that of *Lycopodium Selago*, notwithstanding the heterosporous origin of the prothallus which bears it. A comparison of Fig. 219 with Figs. 207 and 208 reveals a marked resemblance in the form of the embryo when young, and in its first cleavages. In neither is there any marked swelling of the simple spindle-shaped germ, or any distortion; moreover, the relative position of the parts is the same in *S. spinulosa* as it is in *L. Selago*. But the details are not the same in all species of *Selaginella*. For instance, in those where there is a single apical cell the segmentations leading to the definition of the axis are different (Fig. 217): or the position of the root relative to the suspensor, or to the basal wall, is not the same (Fig. 220); and, again, the relative size of the foot may be much greater, while the curvature of the embryo in establishing itself in the soil is also variable. In these respects species of *Selaginella* which have adopted the dorsiventral shoot, and are thus more highly specialised than *S. spinulosa*, appear also to possess greater latitude in the structure and conformation of the young sporeling.

Lastly, in *Isoetes* there is no suspensor: the first cleavage of the zygote is by a wall approximately transverse to the axis of the archegonium; but the embryo is exosepic, as it is also in *Equisetum*, which also has no suspensor. The epibasal hemisphere gives rise to the stem, leaf, and root, while the hypobasal produces only the foot. In fact the zygote, though its polarity is inverted as compared with other Lycopods, behaves as though it represented the embryonic cell of *Lycopodium* or *Selaginella*. These peculiarities will be discussed more fully in Chapter XXVI.

From this comparative summary of Chapters XI to XIV the conclusion emerges that, whether on external form, anatomy, the features of the spore-producing members, or of the prothallus and the embryology, two types stand out respectively from the Eligulate and the Ligulate Lycopods as relatively simple in their characters, and that in many of these features the two types show a remarkable resemblance to one another. They may be exemplified respectively by *Lycopodium Selago*, which is representative of about 40 species grouped as the Sub-genus *Selago* of *Lycopodium*; and by *Selaginella spinulosa*, which is representative of some eight living species of *Selaginella*, grouped as the Sub-genus "*Selaginella* proper." These Sub-genera are of old standing, and were already recognised as generalised in character long before their anatomy, sporangial characters, and embryogeny had been examined in detail. The result of this has been to bring into further prominence their likeness also in many points of detail. The natural conclusion will be that the two great sections of the Lycopodiales converge towards one relatively simple common type. The following verbal specification, based upon the primitive features common to both, may help in visualising a primitive type of Lycopod. The sporophyte would have been radially constructed, possibly unbranched, with relatively small, multifarious and undifferentiated leaves. If branched the shoot would be dichotomous, as also the roots by which it was fixed in the soil. The upper leaves would have been associated each with a sporangium inserted near to its axil, but these would not have been compacted into a definite cone. The conducting system of the adult would have consisted of a non-medullated monostele, with the leaf-traces inserted with the minimum of disturbance upon it. The slightly compressed and stalked sporangia would have been massive and homosporous, the spore-output large, and the dehiscence by a tangential slit. The prothallus would have been conical in form, probably photosynthetic either wholly or in part, with sluggish apical growth, and bisexual: the sexual organs probably arising in acropetal order on a flattened distal region. The embryo produced laterally from it would have been endoscopic, and at first spindle-shaped, with a suspensor cut off by the first cleavage from the embryonic cell; the axis would have originated from its distal centre, and the cotyledons, either successive or of like age, laterally on either side; the root would have been formed laterally, but with its exact position relatively to the other parts uncertain. Lastly, there was probably no specialised intra-prothallial "foot," nor any extra-prothallial "protocorm."

The outstanding feature of that common type, which characterises the Class as distinct from all others, is the relation of the juxtaposed sporangium and sporophyll. This is so constant that the two parts are liable to be thought of as constituting a unit. But is this coalition in any way obligatory? A physiological reason for its constancy probably rests upon the nutrition, protection, and ventilation of the sporangium, and the tissues that nourish it

till maturity, by the subtending sporophyll. This often bears numerous stomata even where it is not photosynthetic, as in the more specialised types. The facts indicate that the relation of sporangium and sporophyll is opportunist rather than obligatory. For instance, the protophylls and the earlier leaves of the sporophyte are barren; some of them may have become so by sterilisation, that is, by abortion of the sporangium—this is certainly the case in the sterile zones of the *Selago*-type—but at the base of the plant there



FIG. 224.

Zosterophyllum australianum: after Lang and Cookson (*Phil. Trans.*, B. vol. 218, Pl. xii., Fig. 16), Incrustation. $\times 2$.

is no need to assume this explanation of the barrenness of the early photosynthetic leaves. They may well have originated independently as such, without sporangia, as they certainly appear to do in living Lycopods. A much deeper interest lies, however, in the converse question, whether sporangia of a Lycopod-type can, or indeed ever did, exist without the subtending sporophylls. A number of plants of the early Devonian Period have lately been described by Kidston and Lang, and others. Some of them have been found to bear on leafless stalks appendages terminated by sporangia, and proved to be such by examination of macerated material and recognition of the spores. Of these the most apposite to the present question is *Zosterophyllum myretonianum*, described as "the earliest known vascular plant from British Rocks," and probably the most ancient fully known land-plant. Here the erect axes, which were without sterile appendages below, bear "characteristic radially arranged, stalked reniform appendages" (Lang, 1927, p. 450; also 1930, p. 158). These were presumably sporangia, but no proof of the presence of spores was at first obtained. This was, however, supplied later in the Australian species, *Z. australianum*, where spores were found united in tetrads within the sporangium (Fig. 224). A re-examination of critical preparations of *Z. myretonianum* disclosed the spores there also. Thus we have full demonstration that in *Z. myretonianum* "the upper region of the branches bore spirally arranged large, shortly stalked sporangia, opening by a slit along the tangentially extended upper and outer edge, and containing spores."

It is not material to our present argument to indicate what may be the phyletic relation, if any, between *Zosterophyllum* and the early Lycopodiales.

What is important is that the existence has been demonstrated in a very early fossil of an axis bearing sporangia of the Lycopodinous type, without any subtending sporophylls. *We conclude then that leaves of the Lycopodinous type may exist without sporangia, and that sporangia of the Lycopodinous type may exist without sporophylls.* It follows that the Lycopod strobilus may be held to be a composite structure, with its constituent appendages essentially independent of one another, though as a rule they are closely related in the cone, as sporangium and subtending sporophyll. This independence finds its analogy in the Equisetales, but there the spore-bearing organs are sporangiophores, and the relation of these to the bract-scales is not so close or constant as in the Lycopods. The discussion of these matters will not be continued further at present. Reference may be made to Chapters XXI to XXIX, where a general comparison of the results of the present detailed analysis will be taken up.

CHAPTER XVI

EXTERNAL MORPHOLOGY OF THE SPOROPHYTE OF THE FILICALES¹

THE Pteridophytes described in Chapters VII to XV are all either leafless, or characterised by possessing relatively small leaves of the type recognised as *microphylls*. Turning now to the Filicales, we encounter under that name the *Megaphyllous Pteridophytes*.² The distinction in foliar habit conveyed by these terms will be fully discussed in Chapter XXVII. Meanwhile for descriptive purposes it may be held provisionally that the leaf in Ferns is large relatively to the axis which bears it, and that its probable origin has been by specialisation of part of an indifferent branch-system: in fact, that it is of *cladode-nature*, and that it owed its origin to distal forking; while the microphyll was from the first a minor lateral appendage.

The Filicales have proved the most successful of the Pteridophytes in establishing themselves as constituents of the current Flora of the Land.

¹ *Selected Literature on the Filicales (General)*: Swartz, *Synopsis Filicum*, 1806. Schkuhr, *Die Farnkräuter*, 1809. Presl, *Tentamen Pteridographiae*, 1836. Kunze, *Die Farnkräuter*, 1840-1854. Bauer and Hooker, *Genera Filicum*, 1842. Hooker, *Species Filicum*, 5 vols., 1846-1854. Hooker and Baker, *Synopsis Filicum*, 1883. Hofmeister, *Higher Cryptogamia*, 1862. Fée, *Mémoires sur la Famille des Fougères*, 1844-1873. Mettenius, *Filices Horti Lipsiensis*, 1856. Luerssen, *Rab. Crypt. Flora*, vol. iii., 1889; the literature on Ferns of Central Europe is fully quoted. Christ, *Die Farnkräuter der Erde*, 1897. Christ, *Geographie der Farne*, 1910; Fern-Floras are fully dealt with. Engler and Prantl, *Natürl. Pflanzenfam.*, i., 4, 1902; literature to date is fully quoted. Lotsy, *Botanische Stammesgeschichte*, Bd. ii., 1909; here literature is fully quoted. Seward, *Fossil Plants*, vol. ii., 1910; here the fossil literature is fully quoted. Campbell, *Mosses and Ferns*, 3rd edn., 1918, with full citation of literature. Scott, *Fossil Botany*, 3rd edn., 1920. Hirmer, *Handbuch d. Paläobotanik*, 1927. Bower, *The Ferns*, vols. i.-iii., 1923-1928. Von Goebel, *Organographie*, 3rd edn., part ii., 1930.

Special Literature for Chapter XVI.: Hofmeister, *Vergl. Unters.*, Leipzig, 1851. ("Higher Cryptogamia," Ray, Soc., 1862). Prantl, *Die Hymenophyllaceen*, 1875. Die Schizaeaceen, 1881. Bower, "Comp. Morph. of Leaf," *Phil. Trans.*, 1884. Potonié, *Naturwiss. Wochenschrift*, Heft 21, 1899. Velenovsky, *Vegl. Morph.*, Prag, 1905. Tansley, "Filicinean Vasc. Syst.," *New Phyt.*, Reprint, 1908. Lignier, *Bull. Soc. Linn. de Normandie*, 1908-9. Schoute, *Konink. Akad. v. Wetensch. te Amsterdam*, 1912. Bower, "Leaf Architecture," *Trans. R.S. Edin.*, 1916. Campbell, *Mosses and Ferns*, 1918, chaps. vii.-xi. Bower, *The Ferns*, vol. i., chaps. iv., v., 1923. Holden, "*Ankyropteris corrugata*," *Phil. Trans.*, B, 218, 1929. Von Goebel, *Organographie*, Teil ii., 1930, pp. 1039-1047, and 1139-1231.

² The life-history of a Fern may be assumed as already known. It is needless to recapitulate its successive events, for they have been already described in *Botany of the Living Plant*, chap. xxxi., and in greater detail in *Ferns*, vol. i., chap. i. (1923).

This is seen to be so whether we accept the criterion of size, or take a census of the individuals in any Flora of a mesothermic hygrophilous type, or again if we estimate the Fern-Population by the number of living genera (about 150), and species (about 6000). They formed an essential feature also in Mesozoic time. Notwithstanding that many fern-like Palaeozoic plants, referred in the first instance to the Filicales on the ground of habit, have been proved to be Seed-Plants, there still remains a fair representation of the Class also among the fossils of the Primary Rocks. In point of propagative power the larger Ferns are supreme among the living Archegoniates, and from their success in competition with modern Seed-Plants they may be held as presenting the highest point attained biologically by homosporous evolution on Land. This result is to be specially associated with the elaboration of the megaphyll, which is habitually a "general-purposes" leaf, serving both for photosynthesis and for propagation. The study of this great Class presents problems of high interest, whether in external form or in internal structure. But it is chiefly the sporophyte generation which has contributed to its success; the gametophyte, though itself adaptable within limits, has never played a leading part. Consequently it is upon the features of the sporophyte that the systematic treatment has always been mainly based. Nevertheless the details of the gametophyte often provide confirmatory evidence of great value. Both will be examined comparatively; but the chief weight will naturally fall upon the sporophyte.

Comparison of Ferns, whether of fossils or of those now living, discloses very considerable differences in size, in general habit, or of inner detail. Most of those types which are prevalent to-day are specialised, and of delicate texture, particularly as regards the exact structure of their minute and very numerous sporangia. They are distinguished as the *Leptosporangiate Ferns*, each sporangium originating from a single parent cell. But certain genera and species, relatively few in number among living Ferns, are more massive, particularly as to their sporangia, each of which originates by outgrowth of a plurality of cells. These are distinguished as the *Eusporangiate Ferns*. Though this distinction is nominally based upon the sporangium, detailed analysis shows that the real difference thus suggested extends to the structure of the plants as a whole; and even to the gametophyte and sexual organs. On the other hand, comparison also shows that these two types, however well marked in extreme cases, graduate into one another by almost imperceptible steps; whether of external form, of structure of the conducting tracts, of the position and grouping of the sporangia, or even of the features of the prothallus, sexual organs, and embryology. Lastly, the palaeontological evidence leaves no doubt on the point that certain Eusporangiate Ferns were of prior existence to the delicate Leptosporangiate Ferns. We are thus in a position to state with some degree of assurance that in the evolution of the Filicales there has been a progressive

refinement of an ancient but more massive type. Nevertheless, the Filicales have remained throughout their descent a very coherent Class of kindred Pteridophytes.

The adult sporophyte consists of a leafy shoot, which may be simple or branched. The leaves of living Ferns are always lateral, and alternate in origin upon a relative axis. But the shoot as established directly from the embryo is at first minute; the earliest leaves are precocious, expanding as photosynthetic organs: that which is first formed is relatively small and simple in outline, but the leaves that follow increase successively in size and complexity of structure till the adult state normal for the species is attained. Meanwhile the stem enlarges also in proportion, and since cam-

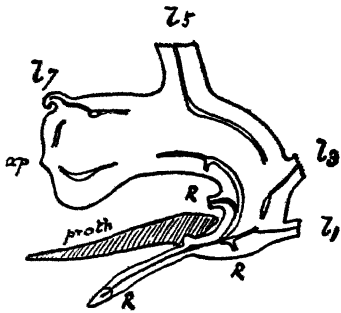


FIG. 225.
Polydodium vulgare. $\times 6$. Median section through prothallus, and embryo, partly diagrammatic: showing one series only of the distichous leaves l_1 , l_2 , etc.; R =roots; ap =apex of axis. The hyponastic shoot becomes completely inverted, growing backwards over the prothallus, and it is markedly obconical upwards.

bial thickening is as a rule absent, its form is obconical (Fig. 225). This is a general feature for the Class, while the absence of secondary growth from Ferns (with very few exceptions) has proved itself a dominating influence over their habit and structure. The sporeling fixes itself in the soil by its first embryonic root, followed by successive secondary roots springing endogenously from the stem. Sometimes a single root may be associated regularly with each leaf-base, as in *Ophioglossum*, or *Blechnum*; but this is not a constant rule: in most Ferns the roots are clearly adventitious in origin, and variable in number. The sporeling thus constructed is capable

of a high degree of individual development; not only may the stem continue its apical growth without apparent limit, but the leaves of Ferns are also endowed in some degree with a similar power. It is associated in them with a feature biologically very apposite for protection of the delicate tip, viz. *circinate vernation*. The elements necessary for the primary enlargement of the individual are thus present, though subject to mechanical and physiological control. In some few Ferns the sporophyte is annual, dying off each autumn: as in *Anogramme leptophylla*, which perennates by a storage-prothallus dormant through the winter; or *Ceratopteris*, where the plant as a whole dies annually, perennation being secured by sporophytic buds. But most Fern-plants are perennial: the seasons impose only a temporary check, often connected in temperate climates with leaf-fall, while a new and enlarged suit of them then appears in each succeeding year. Many Ferns continue indefinitely the simple scheme of enlargement of the shoot thus initiated by the sporeling. This is the foundation of that prevalent

type seen in the common Shield Fern (Fig. 226). In Tree Ferns the further development may be carried to dendroid proportions, with an ever increasing leaf-area borne up on a trunk that may be 60 feet high or more. A practical limit would inevitably be imposed by the deficient power of mechanical resistance of the stem, which is entirely of primary origin, and of unstable, obconical form. But mechanical failure may be staved off by a dense mat of adventitious roots which invests the actual stem, as seen in *Cyathea* or



FIG. 226.

Adult plant of *Dryopteris* (*Nephrodium*) *Filix-mas*, grown in the open. Much reduced.

Dicksonia, and other Ferns in less degree, giving greatly added mechanical support (Fig. 227).

In most Ferns, however, these mechanical risks are avoided partly by their small size, partly also by a creeping habit which is often associated with branching. Dichotomy is the usual mode of that branching. It will be unnecessary here to enter into a detailed analysis of the shoot-system of Ferns.¹ It must suffice to give examples. Fig. 227 shows in transverse section the result of dichotomy in a large trunk of *Cyathea*. In upright-growing Ferns with closely grouped leaves this occurs only occasionally. It is seen, however, in *Osmunda* and *Plagiogyria* among erect Ferns. Dichotomy of the stem is more frequent in those of creeping habit, where the

¹ See *Ferns*, vol. i., chap. iv., where the literature is quoted.

leaves are isolated on a prolonged rhizome. In the Common Bracken it appears early in each sporeling, two equal shanks being formed which immediately burrow downwards into the soil, bearing leaves at intervals (Fig. 228). Either of these shanks may fork again repeatedly, and the result is a widely spread rhizomatous system, embedded in this case in the soil. Another familiar example may be seen in the Oak Fern (*Dryopteris Linnaeana*, C. Chr.) (Fig. 229), where the slender rhizome forks repeatedly; it

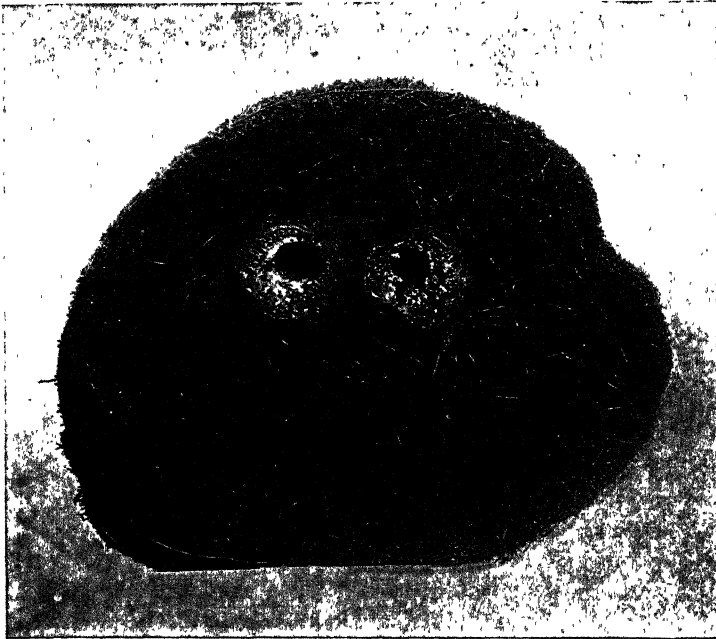


FIG. 227.

Transverse section of a large bifurcated trunk of *Cyathea medullaris*, showing the relatively small size of the twin stems, and the large bulk of the adventitious roots that embed them. Much reduced.

is habitual also in *Lygodium*, *Schizaea*, *Gleichenia*, *Lindsaya*, and *Pellaea* (Fig. 230). Thus dichotomy of the shoot is a recurrent feature in rhizomatous Ferns.

Closely related to the "pose" of the shoot, whether upright or creeping, is its symmetry. The upright shoot is usually radial, while ascending or creeping shoots show varying degrees of dorsiventrality. In Vascular Plants there is strong probability of the erect position having been primitive in the sporophyte, and the prone with dorsiventral symmetry derivative. The arrangement of the leaves on the axis in Ferns, whether radial or dorsiventral, is alternate, a condition initiated in the sporeling, where the first solitary leaf is followed by others arranged on a spiral plan in radial

types; but in creeping Ferns the leaves continue alternate, being inserted right and left, and forming two lax orthostichies. This is well seen in the

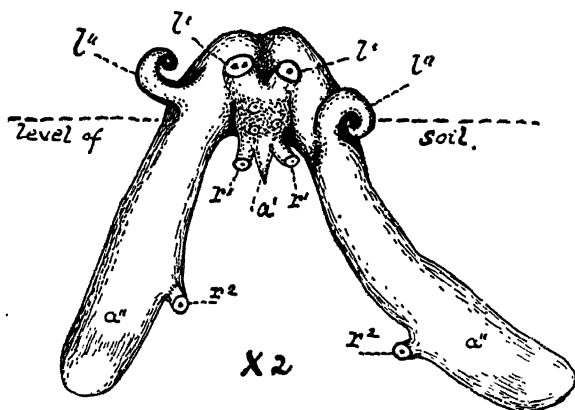


FIG. 228.

Young plant of *Pteridium aquilinum*, seen from the convex, downward directed, side of the curved primary axis, and showing the first dichotomy, with downward directed shanks. *a*', primary axis; *a''*, shanks of first dichotomy; *l'*, leaves borne on primary axis; *l''*, leaves borne on shanks of dichotomy; *r'*, roots attached to the primary axis; *r''*, roots on shanks of dichotomy.

Bracken, and better in *Polypodium Linnæana* (Fig. 229). In ascending or upright stems the spiral leaf-arrangement shows complicated divergences similar to those in Flowering Plants. Sometimes a tendency may be seen towards a whorled arrangement, particularly in certain Tree Ferns; also

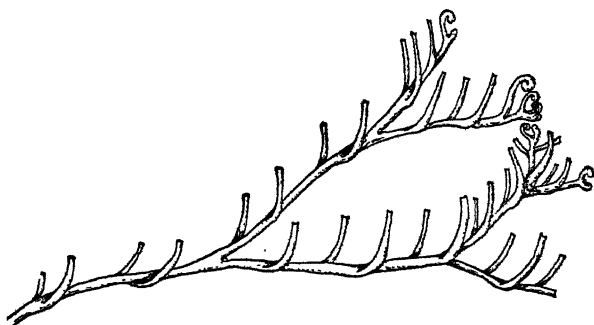


FIG. 229.

Rhizome of *Dryopteris Linnæana*, C. Chr. (= *Polypodium Dryopteris*, L.) dichotomously branched, with alternating leaves, which are cut short at the base. The roots are omitted. After Velenovsky. Reduced.

this appears in the small water-fern, *Salvinia*, notwithstanding that the ontogeny opens with a solitary leaf. Such facts as this last suggest that the alternate arrangement of the leaves is fundamental for Ferns, as against the whorled arrangement in the Articulatae.

In rhizomatous Ferns a very equal forking of the stem may occur apart from any leaf-insertion (Fig. 230). Frequently, however, a leaf may appear to

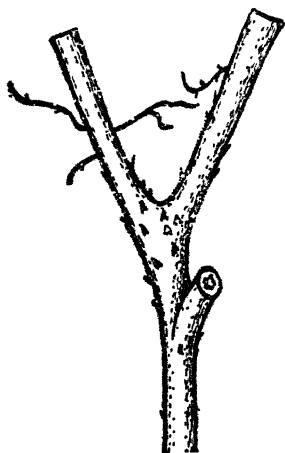


FIG. 230.

Gleichenia (Dicranopteris) fulva, Underw., showing dichotomy of the rhizome. Note the numerous scales, near to the forking, and leaf-base.

be related to it, and it has been stated that the leaf nearest to a dichotomy halves its angle (Velenovsky). That this may be so is not denied; but transverse sections through a number of dichotomising stems, where such an "angular" leaf is present, show that the orientation of the leaf-trace relatively to the branches of the forking stele is inconstant. This fact, taken together with the state seen in Fig. 230, suggests that the forking is a feature of the axis independent of any "angular" leaf, and that the latter, where present, is subordinate either to the original axis or to one or other of the shanks (Fig. 231). Where the development of the two shanks is unequal the relation of the weaker branch to a neighbouring leaf raises questions of high morphological interest. Two special cases may recur with constancy in certain Ferns. The first is seen in certain primitive types, particularly in the Ophioglossaceae and Hymenophyllaceae,

where there appears to be an axillary bud (Fig. 232). An explanation of this is suggested by Fig. 231, *i, ii, iii*: for if one shank of the dichotomy were

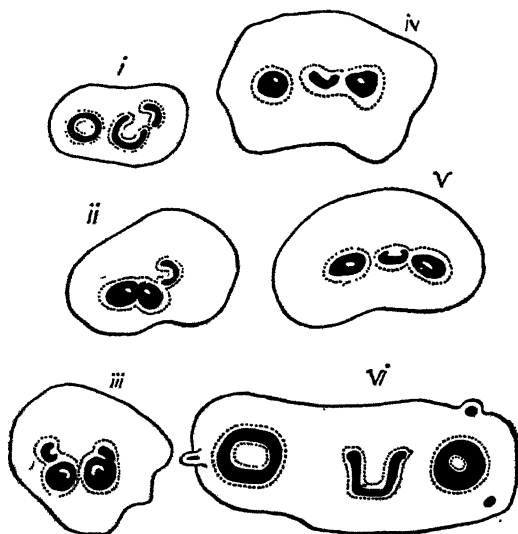


FIG. 231.

Sections from the point of dichotomy of the rhizome of various Ferns, showing the absence of uniformity of relation of the "angular" leaf to the branches of the dichotomy. *i, ii, iii*, suggest that the minor branch is axillary; *iv, v, vi*, suggest that it is dorsal to the leaf. *i, Pellaea falcata*; *ii, Davallia pinnata*; *iii, Davallia tenuifolia*; *iv, Lindsaya reniformis*; *v, Davallia pinnata*; *vi, Paspia viscosa*.

arrested while its first leaf, orientated as in (i), were fully developed, the former would appear as an axillary bud, though the vascular connections would support an interpretation in terms of dichotomy. The advantage of protection of the arrested bud by the leaf-base would tend to perpetuate this feature, and the result would be similar to that now prevalent in Flowering Plants. The second case is seen in *Cheiropleuria* (Fig. 233), *Lophosoria*, *Metaxya*, *Cibotium*, and other Ferns. Here the bud, usually described as adventitious, appears on the abaxial side of the leaf-base. In terms of hypothetical dichotomy the first leaf of the weaker shank would lie in the fork, as it is in Fig. 231, *iv*, *v*, *vi*; and again biological advantage would tend to perpetuate the relation, since the bud could tap the stream of nutriment from the leaf before it reaches the main stem, while it can grow directly outwards from the parent plant. Such branchings, respectively described as axillary and extra-axillary, may thus be resolved in terms of dichotomy; and this reading of them finds its justification in the fact that the relation of the "angular" leaf to the branches is not uniform: this is evident from the sections shown in Fig. 231.

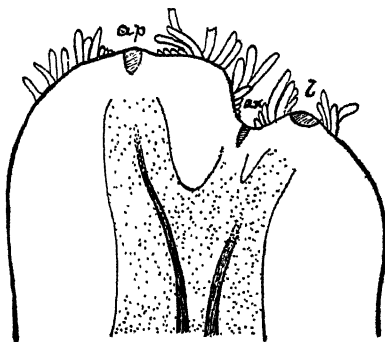


FIG. 232.

Trichomanes radicans, longitudinal section of the apex (ap), with axillary bud (ax), and subtending leaf (l). $\times 20$.



FIG. 233.

Drawing by Dr. J. McL. Thompson of a rhizome of *Cheiropleuria bicuspidata* (Bl), Presl, with its superficial hairs removed so as to expose the successive leaf-bases, which are numbered *Z.i*–*Z.viii*, and the lateral axes which spring from their bases, numbered *ax.i* to *ax.iv*. The leaves *iii*, *vi*, *vii*, *viii*, have no associated axes. The leaf arrangement is alternate, and the climbing shoot is seen from the side facing away from the support. $\times 2$.

The effect of such comparisons is to strengthen the reference of the normal branchings seen in Ferns, even when they appear divergent in detail, to a forking of the whole shoot such as is frequent, especially in those that are rhizomatous. But while we may thus refer many phenomena of bud-formation to original dichotomy, this cannot explain all. There are numerous cases of budding which are clearly adventitious; particularly is this so where the buds arise relatively late upon the upper regions of the leaves, as in the well-known *Asplenium bulbiferum*, or in *Cystopteris bulbifera* (Fig. 234). Consequently the

position remains substantially as it was stated long ago by Hofmeister : that in Ferns the branching of the stem may be referred either to dichotomy, with equal or unequal development of the resulting shanks, or to the formation of adventitious buds. But the line of distinction between these is not always clearly perceptible. This statement appears to be in accord with the conclusions of Schoute (*Konink. Akad. v. Wetensch. te Amsterdam*, Dec. 1912).

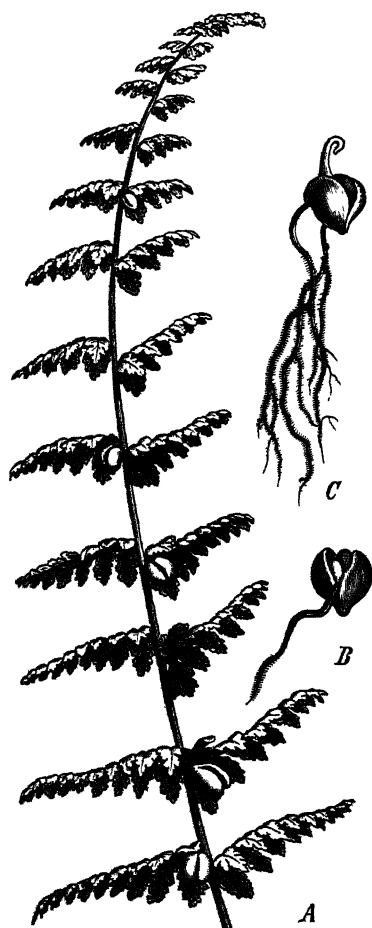


FIG. 234.

Cystopteris bulbifera (L.) Bernh. A=Part of a leaf with adventitious buds, natural size. B=an adventitious bud which has fallen off, forming a root. C=an adventitious bud further developed. B and C somewhat enlarged.

Notwithstanding the morphological interest inherent in the pose, symmetry, and branching of Ferns, these data were not highly valued by the earlier collectors and systematists; and many diagnoses of species are still deficient in the details of the axis, and even of the leaf-stalk. These do not attract the attention of the observer so readily as those of the relatively dominant leaves upon which, and upon the sori and sporangia borne by them, comparison and classification have been chiefly based. The Male Shield Fern provides an average example of the leaf of a Leptosporangiate Fern. It may grow to about three feet in length, and is inserted on the massive ascending rhizome without stipular appendages. The leaf itself consists of a well-marked rachis, or phyllopodium, continuous up to the extreme tip, upon which the numerous pinnae are seated in two lateral rows: these are smaller at the base, rising to a maximum size about the middle, and gradually tapering to a very minute size towards the tip. Though they may

appear to be disposed in opposite pairs at the base they are clearly alternate in the middle and distal regions, and close examination shows that they are really alternate throughout. The pinnae, which may be about 6 inches long in the middle region, are themselves pinnately branched, with more or less clearly alternate pinnules, which may attain a length of about

half an inch, and have a toothed margin (Fig. 235). From a midrib of the pinnule, which is well marked at the base, alternate veins arise, the first being on the anadromic side. The lower veins fork again, but the distal veins do not. Each vein as a rule runs out and terminates in a marginal

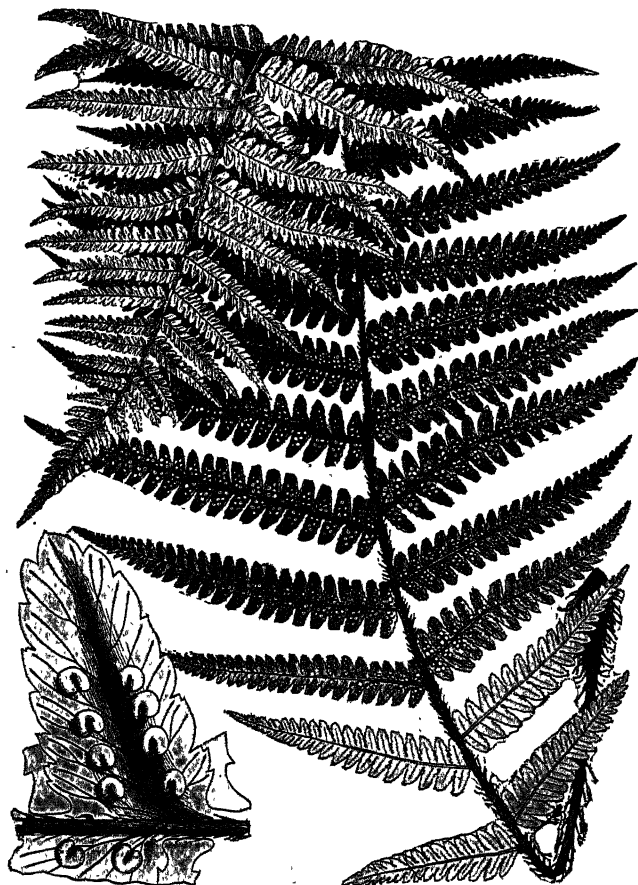


FIG. 235.

Dryopteris Filix-mas, Rich. Fertile leaf about $\frac{1}{2}$ natural size, the lower part with the under surface exposed. To the left a single fertile segment bearing kidney-shaped sori. $\times 7$. (After Luerssen.)

tooth. If the diminishing series of pinnules be followed to the tip of each pinna, or of the pinnae upwards to the leaf-tip, the last minute pinnules or pinnae receive each an alternate vein, in a sequence analogous to that seen in the pinnules' lower down. It thus appears that the underlying plan of construction of the leaf is uniform throughout.

The Male Shield Fern is not a specially primitive type for the Class: its leaves on the face of them bear no clear evidence of the steps by which its

plan of construction may have originated. There are, however, certain features of the branching and venation which point to an underlying system of dichotomy sympodially developed. This is indicated by the consistently alternating disposal of the pinnae and pinnules, as well as by the details of the venation, particularly at the distal region. Further, it is a material fact that all the vein-endings are free though the leaf-segments themselves, whether pinnules or small pinnae, appear each as a continuous expanse, the veins being included. Since the veins retain their sympodial relation below, graduating into dichotomous forking distally, this suggests that the broad surface has originated by lateral webbing of a number of sympodial or forked and veined segments, to form a continuous expanse. The result thus derived from the distal or marginal regions may be followed downwards, and the final conclusion would be that the whole leaf of the Shield Fern has originated from a type consisting of a dichotomous system of narrowly strap-shaped segments sympodially developed. The truth of this suggestion may be tested by reference to the construction of Fern-leaves of simpler type. On the other hand, we may turn to more complex instances with a view to tracing to what further lengths special development may lead. Such comparisons may finally point towards a scheme of leaf-architecture general for Ferns. (Bower, "Leaf Architecture," *Trans. R.S. Edin.*, vol. li., 1916, p. 657.)

There are three lines of argument which may aid our decisions as to the morphology of various types of Fern-leaves along such lines as these : (i) comparison of the details of the adult leaves of different species and genera ; (ii) comparison of the juvenile with the adult leaves of the individual plant ; and (iii) comparison of the related fossils, having regard to their stratigraphical sequence. All of these avenues should be pursued in order to arrive at any final decision ; and if the reasoning from the facts be correct the conclusions from all of them should coincide. In the analysis of foliar structure in Ferns three factors may be recognised as having led to their present state : *Dichotomy* indicated in the adult by the veins, though actually instituted by the distal meristem ; *Webbing*, or *lateral fusion* of shanks or segments, which results in the formation of a coherent blade ; and *Sympodial Development* based upon dichotomous branching, whether in webbed blades, or in those variously cut : it leads to *Overtopping* (*Übergipfelung*). From a biological point of view these three factors are readily intelligible. *Dichotomy* is the most direct mode of amplification of form in plants that follows from the simple sphere, or the cylinder : it is liable to occur wherever there is localised apical growth ; it is prevalent in primitive types, whether in gametophyte or in sporophyte, and it secures an increase of presentation surface in proportion to bulk. *Webbing* is a concession against diffuse form consequent on simple branching. It is seen particularly under conditions of mechanical stress or of excessive surface-exposure : its frequent occur-

rence in subaerial vegetation gives increased mechanical resistance, and regulation of presentation-surface in ventilated plants exposed to wind or drought. *Overtopping* may be regarded biologically as an adjustment following on fixity of position. The problem of the rooted subaerial plant is to make the best use of the dome of space defined by the radius of its spread from the centre of attachment. The greater the height of the organism, and consequently of the radius, the greater the available space; but by overtopping the available space is further increased upwards, or it may be radially outwards. By this means also the creeping or climbing habits have helped Ferns in solving their problem of space in another way.

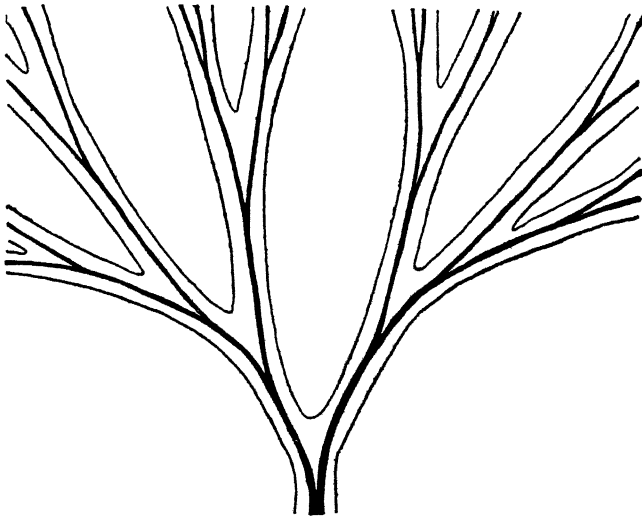


FIG. 236.

Basal part of the lamina of an adult sterile leaf of *Elaphoglossum (Rhipidopteris) peltatum* showing very perfect dichotomy. $\times 4$.

Though *dichotomy* underlies the construction of the leaves of Ferns generally, it is not often seen in modern Ferns in the typical form of equal branching of the veins or of the leaf-segments. This does, however, appear in the adult leaf of *Elaphoglossum (Rhipidopteris) peltatum* (Fig. 236). In *Actiniopteris radiata* also the branching of the veins is diagrammatically regular, but here the lobes are partially webbed. The more complete the webbing the more evident the equal dichotomy appears, as indicated by the veins. It leads naturally to a discoid blade, such as is seen in *Trichomanes reniforme* (Fig. 237). Leaves with their veins thus radiating from the base of the blade are usually long-stalked, and inserted singly upon a creeping rhizome. This seems to be a condition of success of that simple scheme which could not be continued to a large size to produce an effective photosynthetic organ where the form of the shoot is compact. Herein probably

lies the reason why a scheme of equal dichotomy is rare in the adult, and never attains large size.

The third factor above named comes in to meet this difficulty of size, viz., *sympodial development* or *overtopping*. The steps by which it may be established as the size increases are well illustrated in successive juvenile leaves of *Osmunda*, which present details of branching of the veins though

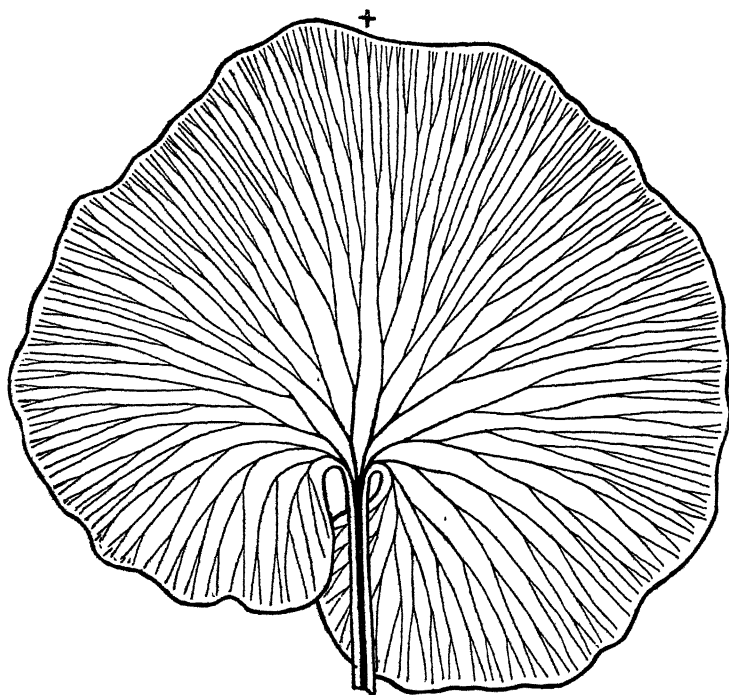


FIG. 237.

Leaf blade of *Trichomanes reniforme*, showing detail of venation, and its vascular connections downwards to the petiole. + marks the limit between the right and left halves of the dichotomy. Drawn by Dr. J. McL. Thompson. Natural size.

the blade is fully webbed (Fig. 238). In the cotyledon the single strand of the leaf-stalk forks as it enters the lamina, and each shank forks again twice (*a*). Successive older leaves (taken here from different plants) show at first striking equality of lobation and of dichotomous venation (*b-d*). But passing to older and larger leaves the equality is gradually lost: thus in (*e*) the left lobe is the larger, as is also the acroscopic shank of its venation, thus showing a tendency to sympodial development, while the lobe itself is divided into two parts, that which is acroscopic projecting the farthest. In (*f*) this part has assumed a pseudo-terminal position, with its venation sympodially developed. In (*g*) there is a clearly defined terminal lobe, with its venation apparently of distal origin. Nevertheless at the tip of each lobe or

pinna the venation remains equally dichotomous. In older leaves the terminal leaflet and lateral pinnae become more clearly defined, and are them-

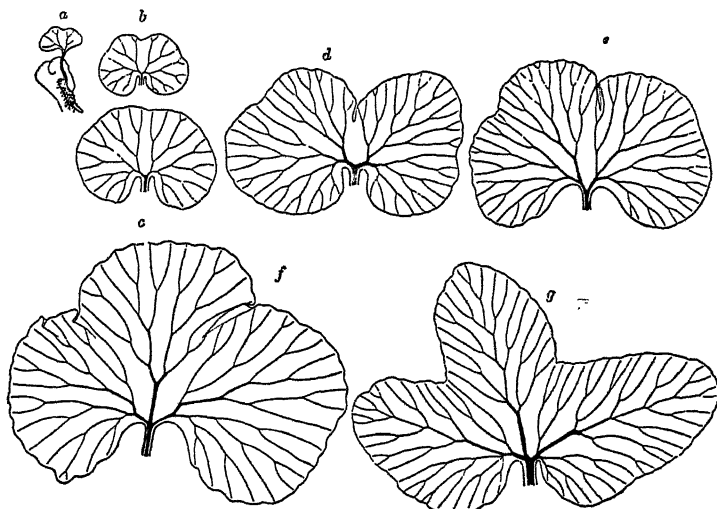


FIG. 238.

Successive juvenile leaves of *Osmunda regalis*, showing successive steps of progression from equal dichotomy to symphyllal branching, and the establishment of a terminal lobe. $\times 2\frac{1}{2}$.

selves liable to similar lobing, till in the adult state the highly divided leaf of *Osmunda* is reached, with its rachis bearing two rows of compound

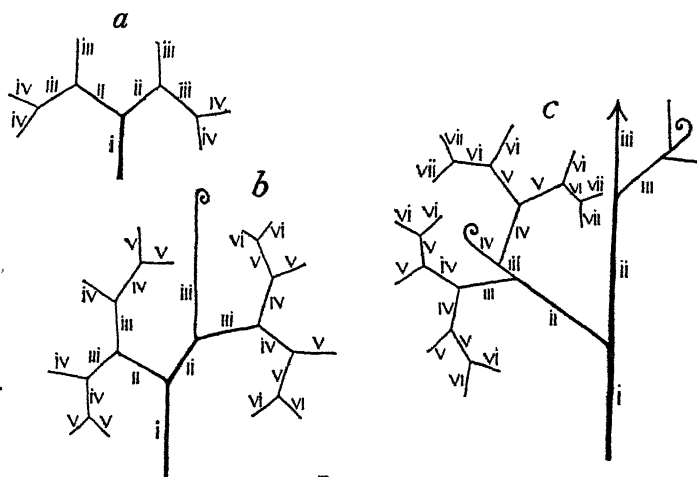


FIG. 239.

Schematic drawings, after Prantl, showing the symphyllal development in leaves of *Lygodium circinatum*. a, b, c, show successive steps from equal dichotomy to symphyllal branching.

pinnae. This progression with increasing size illustrates how the pinnate type of leaf in Ferns originated. It may be followed with equal clearness in

Todea, or *Anemia*, or in *Cyathea* (*Ferns*, vol. i., figs. 76, 77, 97). In all of these the leaves are more deeply cut than in *Osmunda*, the lobes according generally with the branching of the veins. Such illustrations will suffice to suggest the effect of sympodial development of dichotomous branching in relatively primitive Ferns. Comparison shows that this has been the leading factor in the architecture of them all, even the largest and most elaborate.

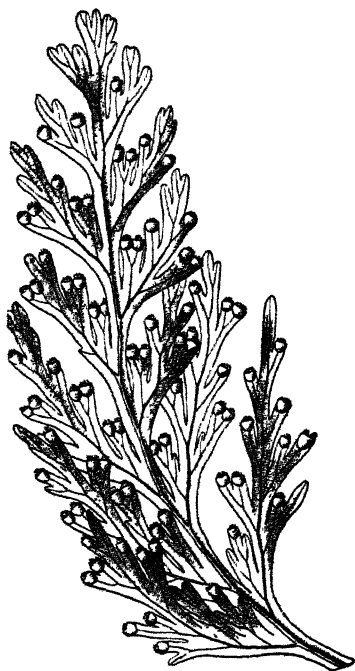


FIG. 240.

Habit of leaf of *Hymenophyllum dilatatum*; the single incised segments are separate one from another, which is regarded as a primitive state. (After Sadebeck.)

The progression from equal dichotomy to the sympodial state was first worked out by Prantl in *Lygodium circinatum*, one of those climbing Ferns which have unlimited apical growth of the leaf.¹ He illustrated the ontogenetic stages, as seen in successive leaves, by the diagrams shown in Fig. 239, which prove to be very generally applicable to relatively primitive and simple Ferns.

The dichotomous branch-system developed sympodially, as in *Osmunda* or *Dryopteris*, is described as a *scorpioid dichopodium*, involving the establishment of a pseudo-axis. This scheme underlies the structure in the great majority of Fern-leaves; but it is subject to varied modifications. In each case the evidence of what has happened may be traced either in the outline of the leaf or pinna, or more certainly by the venation, or by both combined. A few examples will serve for illustration.

A very prevalent state in early Ferns is that known as the *Sphenopteris*-type, where the leaf is finely divided into narrow segments, each with a single median vein. It survives in *Todea superba* (*Ferns*, i., fig. 76), and especially in the Hymenophyllaceae (Fig. 240). Such segments may be grouped into a complicated sympodial structure, with marked midrib and pinnae. In *Trichomanes* the first leaf of the sporophyll resembles one of these ultimate lobes (*Ferns*, ii., fig. 516). *In fact the adult leaf is built up from the first on the basis of the single-veined unit. But frequently the steps of development of the dichopodium may be curtailed at the outset.* This is seen in *Helminthostachys* and *Botrychium* (Fig. 241), where the earliest stages are omitted, and the cotyledon itself presents a venation comparable to that of the sixth

¹ Prantl, *Die Hymenophyllaceen*, Leipzig, 1875; *Die Schizosaceen*, Leipzig, 1881.

stage of *Osmunda* (compare Fig. 241, *B*, with 238, *F*). The Ophioglossaceous cotyledons have each a distal lobe and two pinnae: it is notable how similar is the venation in both; this suggests that in closely related forms

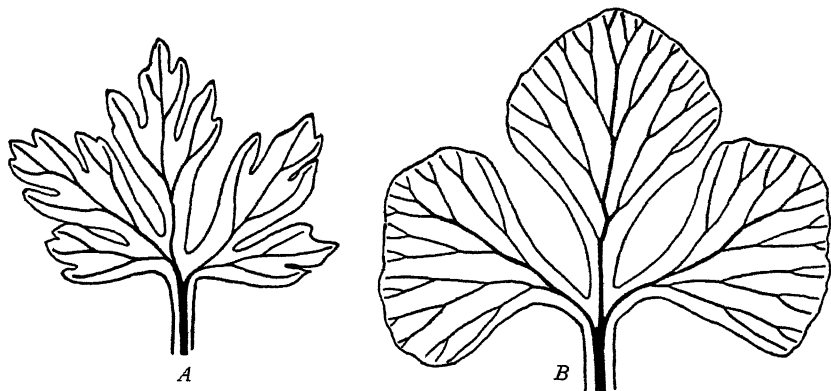


FIG. 241.

A, cotyledon of *Botrychium virginianum*. *B*, juvenile leaf, probably the cotyledon of *Helminthostachys*. In these the ontogeny starts from a relatively late stage, as compared with *Osmunda* or *Anemia*. $\times 4$.

the scheme of branching is not directly dependent on the degree of webbing. On the other hand, the adult leaf of *Angiopteris* illustrates how the system of branching may be curtailed at the distal end. Before this can be fully understood it will be necessary to describe briefly the detail of distal branching as it is seen in the leaves of most Ferns.

Where the scorpioid structure is strongly developed, with a marked rachis or phyllopodium, a succession of alternating pinnae is commonly produced, as in the Shield Fern, or any of our native types. In such cases, if the actual development of the individual leaf be traced, the primordia of the earlier pinnae are found to arise below the growing apex of the leaf, appearing as lateral outgrowths upon it (Fig. 242). The branching is thus in point of fact monopodial. But as the apex of the leaf is approached there

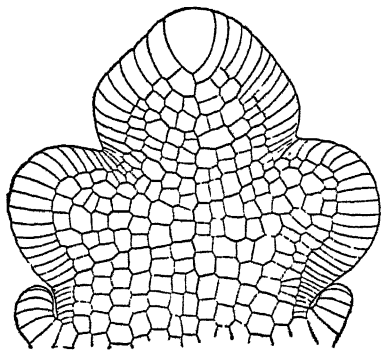


FIG. 242.

Young leaf of *Ceratopteris* seen in surface view, showing apical segmentation. (After Kny.) The alternating pinnae, which arise monopodially, do not correspond to the segments cut off from the apical cell.

is a gradual approach to sympodial dichotomy, and finally it may be to equal dichotomy of the apex. The type of cellular cleavage at the extreme distal margin is shown for the leaf of a sporeling in Fig. 243, while the diagrammatic representation of it as an equal dichotomy is shown in Sadebeck's

drawing. There is in fact in the early stages of ontogeny of many adult Fern-leaves a monopodial branching which produces the lower pinnae or pinnules. This is a later and derivative type of branching. But there is a

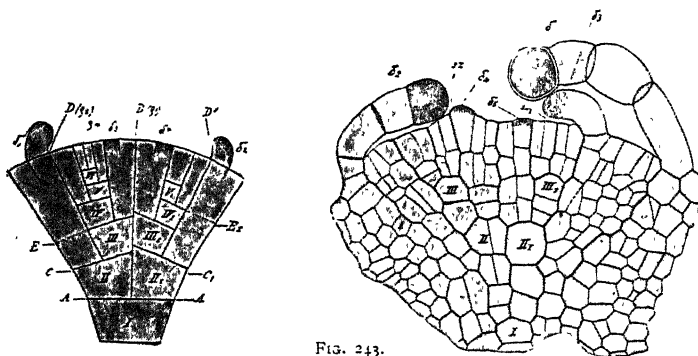


FIG. 243. Portion of the leaf-surface of a sporangium of *Asplenium serpentini*, showing how dichotomy accompanies the marginal growth. $\times 190$. To the left is a diagrammatic representation of the same. (After Sadebeck.)

transition from this by gradual steps of distal approach to sympodial dichotomy, and finally to equal dichotomy, such as is characteristic of juvenile leaves. Consequently, if the phyletic history be reflected in these changes, the series would have to be taken in reverse of that actually seen in the development of the individual leaf, and the evolutionary succession of steps would read thus: (i) equal dichotomy; (ii) sympodial dichotomy; (iii)

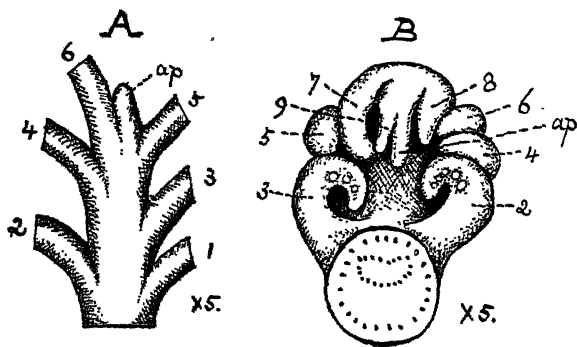


FIG. 244. Young leaves of *Angiopteris*. A = apex of leaf, bearing six alternate pinnae. The phyllopodium ends abruptly in a cone, ap. $\times 5$. B = apex of a younger leaf with alternating pinnae, 2-9, formed by monopodial branching. ap = apex. The pinnae, 2, 3, have begun to form pinnules, also monopodially.

monopodial branching. This succession probably reflects truly the steps in the phyletic elaboration of foliar structure in Ferns.

This general view may now be applied to the case of *Angiopteris*, where the adult leaves are of large size, and doubly or trebly pinnate, but with relatively few primary pinnae borne upon a massive phyllopodium (*Ferns*,

ii., Fig. 388). In the Marattiaceae the sporeling leaves may at first show equal dichotomy, leading soon to the scorpioid dichopodium, which applies for all stages up to the adult leaf ("Leaf Architecture," *Trans. R.S.E.*, 1916, Figs. 10, 11). In early stages of the latter the primary pinnae arise by monopodial branching, but in *Angiopteris* they are few in number, e.g. 16 or less. Here the transition to the sympodium is not made clear owing to arrest of the apical growth of the phyllopodium. Its tip appears then as a blunt cone, and all the primary pinnae being of monopodial origin, the primary branching resembles that seen in the leaves of Cycads, or of many pinnate Angiosperms (*ap.* Fig. 244, *A, B*). The explanation of this for

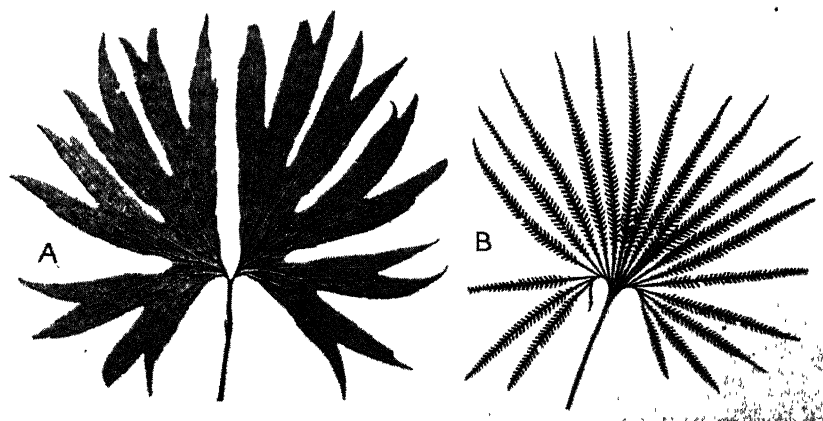


FIG. 245.

A, Leaf of *Dipteris conjugata*, showing anadromic helicoid structure. Much reduced.
B, Leaf of *Matonia pectinata*, showing catadromic helicoid structure. Much reduced.

Angiopteris is based upon comparison of its juvenile leaves : it is concluded that the construction throughout is essentially dichopodial, but that in the adult the distal growth is arrested before the normal reversion to the primitive branching had been reached.

The dichopodium thus established may be worked out in adult Ferns in various ways. The commonest is by the promotion alternately of the right and of the left shanks of the forking over the other. The result is a straight or slightly zig-zag *scorpioid dichopodium*, well shown in *Dryopteris Filix-mas*. It apparently continues the leaf-stalk, and the two together constitute the rachis or phyllopodium (Fig. 226). Frequently, however, the promoted shank may not lie alternately right and left, but be continuously repeated on the same side : this gives the type of *helicoid branching*. There are two types of this : in one the promoted shank is constantly on the anadromic side, i.e. that directed towards the leaf-apex ; in the other it may be on the catadromic side, i.e. that directed towards the leaf-base. The former is seen in *Dipteris*, the latter in *Matonia* (Fig. 245, *A, B*). Similar features

often appear locally in the branching of Fern-leaves which do not show helicoid branching throughout. Thus by variations of the balance of helicoid branching—all derived ultimately from dichotomy, and combined with different degrees of webbing—there may arise great diversity in development of the leaves of Ferns.

The types of leaf-structure so far discussed have as a rule *open venation*: many even of those broad leaf-areas referable in origin to webbing may present free vein-endings. This state is characteristic of early types, such as *Botrychium* and *Helminthostachys*, *Marattia* and *Angiopteris*, *Schizaea*

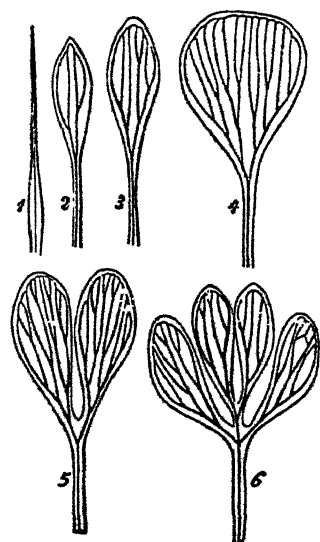


FIG. 246.
Successive types of juvenile leaves of *Marsilia* with dichotomous veins connected by marginal loops. (After Braun.)

and *Gleichenia*, and almost all of the Hymenophyllaceae and Cyatheaceae. But departures from this simpler and physiologically less efficient state are frequent, and often occur in certain species or genera of primitive groups. Thus *Christensenia* among the Marattiaceae, and *Ophioglossum* among the Adder's Tongues have reticulate venation; or within the genus the sections *Anemidictyon* and *Hydroglossum* are reticulate types respectively of the genera *Anemia* and *Lygodium*. Reticulation appears to be a structural amendment which has originated polyphyletically in a number of distinct families of Ferns. A very simple step towards a closed venation consists in the formation of marginal loops, resulting in a continuous intra-marginal commissure, such as is seen in *Marsilia* (Fig. 246). But fusions may be initiated in other ways, leading to more elaborate reticulation, and

finally to small-meshed networks. There is some evidence of an ontogenetic progression from an open to a closed venation: the first leaves of *Ceratopteris* may be without fusions, though these appear in the later leaves. But usually where reticulation exists in the adult it is established in the earliest leaves of the individual, as in *Cheiropleuria* or *Platyserium* (Fig. 247). Nevertheless it may be held that, so far as it goes, the ontogenetic evidence indicates that open venation is a primitive and closed a derivative state.

More cogent evidence comes from the stratigraphical sequence of fossils. Reticulation is unknown in plants of the Devonian period. Potonié notes that Stur does not record a single instance of reticulate venation even from the Flora of the Culm. Meshwork is first seen in the Middle Coal Period, though many of the examples of it that have been quoted are now ranked as Pteridosperms. It is not till the Mesozoic Period that reticulation

of a high order—that is, with a smaller network within the larger meshes—became prevalent. This state is well illustrated by *Clathropteris egyptiaca* (probably a Pteridosperm) from the Nubian Sandstone, which has a venation that may be matched by many modern Ferns (Fig. 248). From such facts it seems to follow that open venation was primitive, and that reticulation with progressively smaller meshes was derivative. The physiological advantage gained by intimate vein-fusions in promoting equal distribution over large leaf-areas gives added probability to this conclusion. The detailed

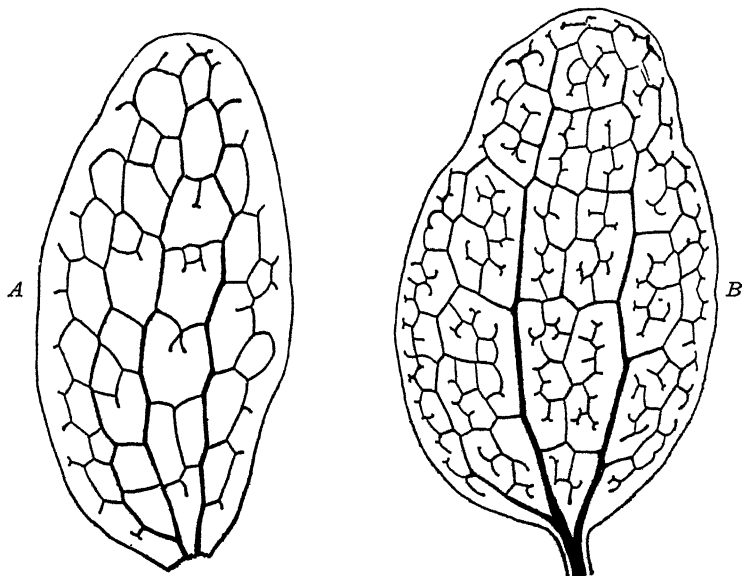
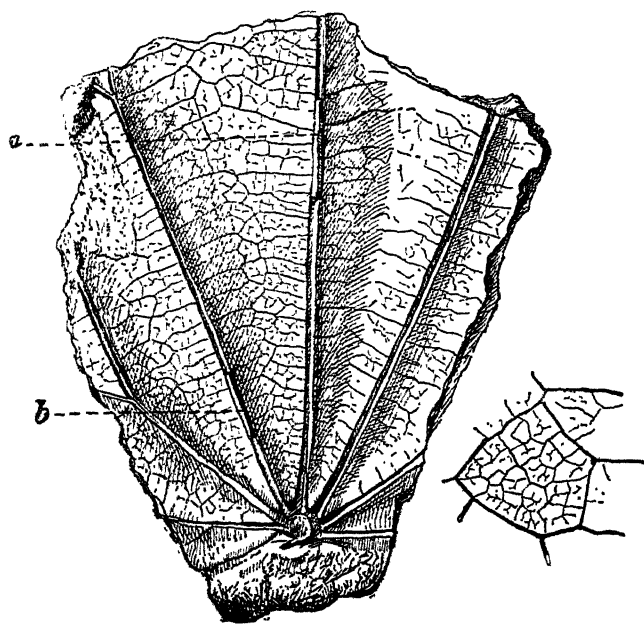


FIG. 247.
Juvenile leaves, already showing reticulation. A, in *Platycerium*. B, in *Cheiropleuria*.
× 3.

arrangement of the veins in the leaf-blade of Ferns has been widely used in their systematic arrangement. This has led to a special classification and terminology, together with elaborate descriptions of the various types. It will not be necessary here to enter further into these details. An examination of the several types will show that they may all be traced back along the lines above explained to a simple dichotomous venation, equally or more often sympodially developed.

The disposal of the pinnae along the rachis depends chiefly upon its intercalary growth. When it is feeble and equally distributed the result will be two close rows of pinnae, as in the Shield Fern (Fig. 226). If the intercalary growth be strong between the pinnae, and combined with long-continued apical growth, the result may be leaves of great length, which straggle or climb to considerable heights above the creeping rhizome: this is seen in *Lygodium*, *Gleichenia*, and *Odontosoria* (*Ferns*, vol i., Figs. 43,

44). But where equal dichotomy prevails the growth is localised below the first forking, and the blade is carried bodily up on a long stalk, as in *Trichomanes reniforme* (Fig. 237). On the other hand, an intercalary zone may intervene above certain pinnae, which are then left at the leaf-base. This is sometimes seen in the Cyatheaceae, and particularly in *Hemitelia capensis*, where the modified basal pinnae have been dubiously described as "aphlebiae." There is no need to see in such organs a special category



1

FIG. 248.

Clathropteris egyptiaca, natural size, from the Nubian sandstone, with radiating main ribs, connected by fine reticulate venation. (After Seward.)

apart from other segments of the leaf-blade, but rather to look upon them as specialised types of pinnae. This explanation, however, will not account for all growths found at the leaf-base. Certain primitive Ferns bear "stipules": for instance, the Ophioglossaceae, Osmundaceae, and Marattiaceae. These appear as lateral outgrowths on the leaf-primordium, with or without a commissure connecting them across the face of the leaf-stalk, and thus forming an efficient cover for the next younger leaf. This commissure is present in *Angiopteris* (Fig. 249), *Marattia*, *Christensenia*, and *Todea*, but it is absent in *Osmunda*, where only lateral flaps are formed. Such basal growths are probably of distinct phyletic origin from the distal branchings. They are absent from all advanced Filicales, though represented in the

Pteridosperms and Cycads. If they are referable, through basal aphyllae to a normal branching, their origin must have been very far back in the evolutionary history.

The various types of Fern-leaves show, perhaps as well as those of any Class of Plants, how evolution can play variations on a given structural theme. In the leaf of Ferns the widest resources of an essentially dichotomous plan are tapped, as regards *external form*. In strange antithesis the stems of Ferns exhibit a like resource in the play upon *internal stelar structure*, while their form remains consistently that of the inverted cone. The one is complementary to the other, and given an absence of cambial thickening, the stelar vagaries of the Fern-stem seem to be a natural corollary upon the elaboration of the enlarging leaf. This subject will be taken up again in Chapter XXVIII.

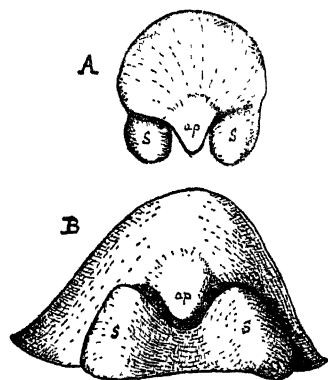


FIG. 249.

Young leaves of *Angiopteris* before the formation of the pinnae. *A*, as seen from above, *B*, as presenting the adaxial front. *ap*=apex of the phyllopodium; *s*=stipules. $\times 10$.

Among the earliest fossils attributed to the Filicales, or recognised as akin to them, more elaborate leaf-structure is sometimes found than in living

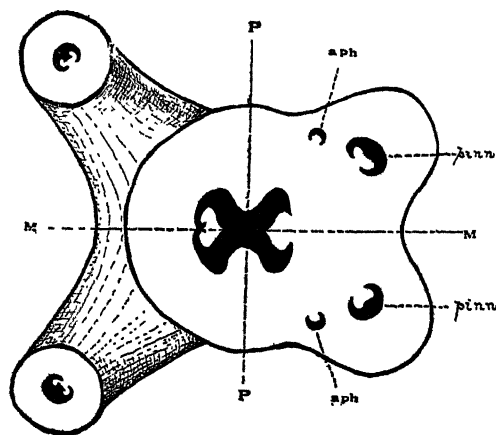


FIG. 250.

Diplolabis Romeri, Solms. Diagrammatic drawing showing the ramification of the primary petiole, as it might be seen in a thick transverse section. *P, P*, principal plane of symmetry. *M, M*, median plane. *aph*, aphyllae-trace; *pinn*, pinna-trace. (After Gordon.)

Ferns: there is also evidence in some of them of a less clear differentiation between leaf and axis. In the Coenopteridaceae the stems were either upright with crowded leaves, or rhizomatous with isolated leaves. But the actual form of the leaves is often imperfectly known, particularly in the Botryopterideae. In the Zygopterideae the leaves were relatively large, and probably upright in habit, consisting of a rachis traversed by a complex meristele, branches from which supplied the pinnae. These were arranged either in two lateral rows,

as in modern Ferns (*Clepsydroopsis*, *Asterochlaena*); or in four rows, as in the Dineuroideae (Fig. 250). The pinnae, where they were flattened, appear to have been orientated in planes transverse to that including the axis of the leaf,

while in modern Ferns the plane of the pinnae includes the axis. In *Diplolabis*, and others, the pinnae were disposed in equal pairs, as though each pair originated by dichotomy from a single lobe, while further subdivision followed. This mode of branching was deeply stamped on the frond of *Stauropteris*, a frequent fossil of the Coal Period. Its stem is unknown : the frond has been described as a feathery plexus of green branchlets devoid of lamina, some of which bore terminal sporangia (Seward). The mode of origin of these branches is comparable in position with those of *Diplolabis*, but their branching has been carried forward to a second, third, and even a

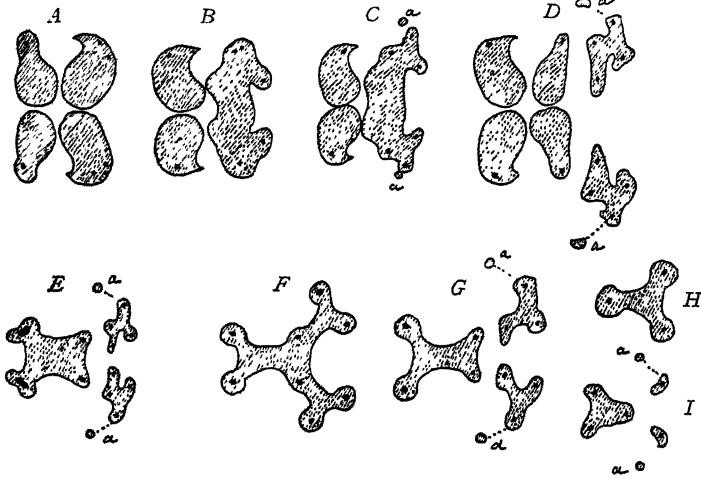


FIG. 251.

Vascular supply to the ramifications of *Stauropteris*, after P. Bertrand. The protoxylem is represented by black dots. A, a rachis of the first order, showing a mean condition of the four xylem-traces; B, C, D, stages in the departure, on the right, of the supply to two pinnae of the first order; a, aphlebia-traces; E, rachis of the second order, showing undivided xylem, from which pinna-traces of the second order have been detached, with their aphlebiae (a). F, G, stages in the departure of triangular traces for pinnae from the triangular xylem-trace of a rachis of the third order; H, triangular trace of the fourth order; I, the same, giving off traces to pinnae and aphlebiae (a). Compare Fig. I with Figs. D, E, G, which together illustrate the progressive simplification of the smaller branchlets. It is on the ends of these that the sporangia are borne.

fourth order ; thus giving a high degree of subdivision of the branchlets. It has been traced by P. Bertrand by means of the vascular system, with results as seen in Fig. 251, and explained in the rubric. So long as the base of this problematical plant is unknown it is impossible to say what relation its complex frond bore to other parts. It may perhaps represent the chief organ of a plant in which the distinction of leaf and axis was not existent. If that were so a comparison with the *Asteroxyleae* would appear to be apposite. In any case these early types present a complex condition in which the frond, or leaf, has not settled down to that confirmed bifacial structure which is characteristic of leaves that are related to an axis.

All the families of Ferns, even the *Ophioglossaceae* and *Marattiaceae*, bear *dermal appendages* of some sort ; but though these are very constantly present on the youngest parts they often fall away at maturity, giving the

effect of a bald surface. The simplest are unbranched, being derived by outgrowth of a single cell, followed by transverse partitions only : this gives a linear series of cells (Fig. 252, 1). The distal cell often develops as a gland yielding a secretion, as in *Notholaena*, or *Gymnogramme*; frequently it contains mucilage, as in the Osmundaceae and Blechninae, which is protective to the young parts (5). The structural elaboration of hairs possesses comparative interest. The simple linear hair is characteristic of many

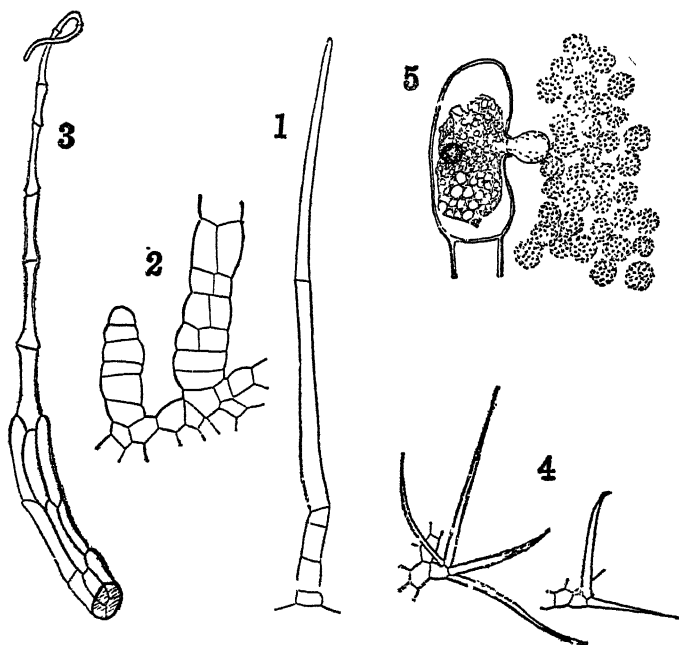


FIG. 252.

1, Simple hair of *Matonia*, after Seward. 2, Hairs of *Dipteris conjugata*, with occasional longitudinal divisions near the base, after Seward. 3, Hair with massive base, of *Dipteris Lobbiana*. 4, Stiff stellate hairs of *Trichomanes alatum*. 5, Mucilaginous hair of *Blechnum occidentale* discharging mucilage from its distal cell. (After Gardiner and Ito.)

primitive types : such as the Ophioglossaceae, Osmundaceae, Dicksonieae, and Matonieae ; and notably it is present in certain genera recognised as synthetic types, for instance, *Loxsoma*, *Plagiogyria*, *Lophosoria*, and *Metaxya*. In certain Ferns the basal cells may show longitudinal partitions, so as to constitute a stiff bristle, as in *Dipteris* (2, 3), and this is seen in *Ankyropteris* (Holden). It may be carried further to the formation of massive emergences, particularly about the leaf-base, upon which the hair may be borne outwards from the surface, as in *Gleichenia* (Fig. 253). If the hair be itself branched, as often happens, there are two alternatives. Either the branches remain separate (Figs. 252, 4 ; 253), or they may be webbed so as to form a flattened scale. Intermediate stages show that the latter is a

derivative state (Fig. 254). Such scales are often peltate round a stalk of insertion which may be massive, particularly at the leaf-bases of the Cyatheaceae. The expanded scales themselves, which overlap while young, forming a very complete protection, usually fall away from the adult stem or leaf, leaving the massive stalk as a permanent spine. As an accessory basis for comparison hairs and scales yield useful evidence.

The roots of Ferns are mostly fibrous, though inclined to be fleshy in the Ophioglossaceae and in some other primitive forms. Their origin is adventitious, and their branching is as a rule monopodial. Exceptions to

this are, however, found in *Ophioglossum*, where their vascular structure may be monarch, especially close to the insertion. Their branching may be either terminal and bifurcate or monopodial. It was suggested by Van Tieghem that dichotomy is restricted to the monarch roots, and that we know beforehand if the root is monarch that it will dichotomise (*Ann. Sci. Nat. V. Série*, T. xiii., p. 108). Such facts have a special interest for comparison with the bifurcate and monarch roots seen in Lycopods.

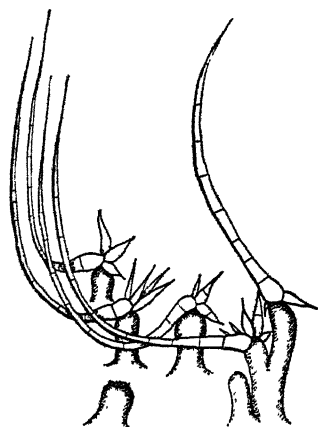


FIG. 253.

Hairs from the base of the leaf of *Gleichenia pectinata*. Each is seated on a massive emergence, from which it is easily detached, the emergence remaining as in the Cyatheaceae. $\times 50$.

In this comparative study of development of the stems, leaves, and roots of Ferns it has been seen that in all of these members dichotomy has played its part. Moreover, an equal forking is more prominent in those which have on general

grounds been held as relatively primitive. But its regularity has been seen to give way by gradual steps, first to sympodial development, then to the establishment of a scorpioid dichopodium, and finally to monopodial branching where the parts of higher order arise as lateral outgrowths below an established apex. Thus the Ferns, perhaps more clearly than any other Vascular Plants, illustrate a transition from that type of branching which is characteristic of a lower organisation towards that which is firmly established in the Higher Plants. It has even been seen how an axillary position of a bud may be read in terms of dichotomy (*Trichomanes*, Fig. 232), and how a leaf, with all its pinnae originating monopodially on the phyllopodium, may also be referred to a like source (*Angiopteris*, Fig. 244). Such conclusions do not justify the statement that all monopodial pinnae and all axillary buds of Flowering Plants have originated in this way; but the facts derived from Ferns do certainly lend countenance to the view that such may have been their source. Those facts suggest also a very important

further step. We may apply the analogy of the gently graded origin of monopodial pinnae in Ferns, from a dichopodial development of dichotomy, to the origin of leaves monopodially upon an axis. A study of the origin in Ferns of lateral pinnae upon the phyllopodium from an indifferent dichotomy suggests that the megaphylls themselves may have originated in the same way from an indifferent source, which gave rise also to the axis. This theory was first stated in 1884, not as an idea lightly thrown out, but as a

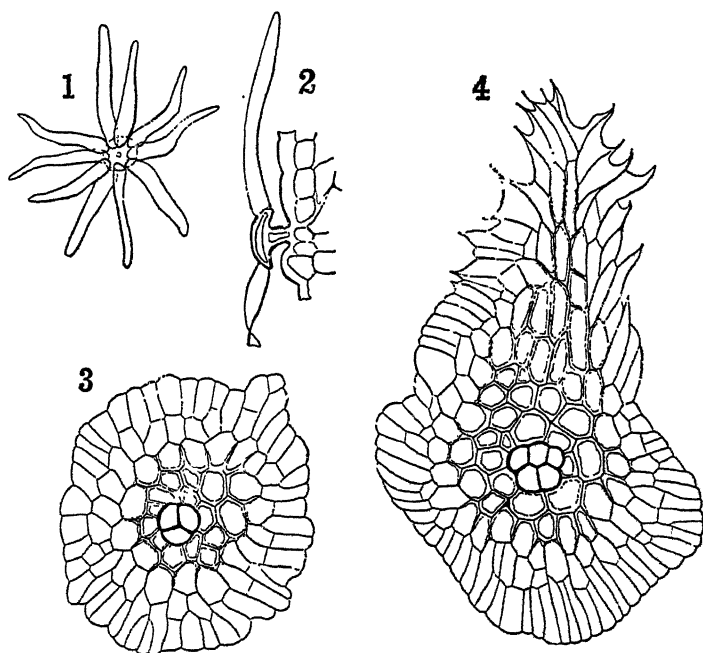


FIG. 254.

1, 2, Stellate hairs of *Polypodium lingua*. 3, 4, peltate scales of *Polypodium incanum*. $\times 65$.

legitimate induction from a study of leaf-development in the Vascular Cryptogams and Gymnosperms (Bower, *Phil. Trans.*, 1884, part ii., p. 565). A similar suggestion was made later by Potonié, in the thesis that the leaves of the Higher Plants sprang in the course of generations from thalloid segments, through the dichopodial development of dichotomous branching: and thus the branches became leaves (Potonié, *Naturwiss. Wochenschrift*, Heft 21, Berlin, 1899). His argument was chiefly based upon comparison with Algae, in which it is true dichopodial development is frequently seen. In 1908 Tansley restated this thesis, but he supported it on more valid grounds. Anatomical comparison of axis and leaf-stalk in certain early vascular types suggested to him a common origin ("Filicinean Vascular System," *New Phyt.*, Reprint, 1908, p. 3). All these comparisons were founded on analogy rather than on any positive chain of facts; for no plant had at

these dates been found which clearly indicated, within a reasonable circle of affinity, a distinction of stem and leaf in the making from an indifferent dichotomy. With the disclosure in recent years of new and very perfect specimens of the early Devonian Flora the whole attitude to this question has altered, and the field of argument is now being rapidly filled in by positive fact. The discussion of such questions will be taken up in Chapter XXVII, and a restatement will there be made of a theory of origin of the cladode-leaf, as it is seen in the Filicales. Meanwhile it may be held, as a working hypothesis, which accords with known facts, that the cladode-leaf or megaphyll had a dichopodial origin from an indifferently dichotomous shoot not yet differentiated into axis and appendage. But the dermal appendages present on axes and cladode-leaves, such as hairs and scales, even when largely developed, are of the nature of surface enations, and show no evidence of a distal dichotomous origin. Moreover, in Ferns they are only rarely photosynthetic. It thus appears that the whole shoot-system of Ferns is referable in origin to: (i) distal dichotomy of an indifferent vegetative system, which has given rise to axis and cladode leaf; (ii) occasional adventitious budding of supernumerary shoots; and (iii) enation of minor appendages.

CHAPTER XVII

ANATOMY OF THE FILICALES¹

PRIMARY SEGMENTATION

THE term Anatomy may be read as including the study of apical segmentation as well as that of the adult tissues. From the analysis of the meristems of Ferns justification will be found for their seriation from the relatively ancient and massive Eusporangiatae to the relatively modern and delicate Leptosporangiatae. In the former the collective tissues of the adult part are not traceable back with constancy to the segmentation of a single initial cell, but there are usually 2-4 of them; while in the Leptosporangiates one initial with regular cleavages is found to be their source. There is, however, no sharp line of demarcation between the two types in respect of such details: there are Ferns now living which show an intermediate state, notably the Osmundaceae, whose history dates back to Permian times. In this respect these relatively primitive Ferns take their place as a synthetic group, linking together the ancient Eusporangiate and the more modern Leptosporangiate Ferns into a coherent sequence of kinship. It will be found, as we proceed with our analysis of apical meristems, that this kinship is borne out not only by the adult anatomy but also by the features of the propagative organs.

¹ *Selected Literature for Chapter XVII. (Segmentation):* Kny, *Parkeriaceae*, Dresden, 1875. v. Sachs, *Anordnung d. Zellen*, Würzburg, 1877. Schwendener, *Sitz. d. K. Preuss. Akad. Wiss.*, 1882. Von Goebel, *Vergl. Entw. Schenck's Handbuch*, iii., 1884. Klein, *Bot. Zeit.*, 1884, p. 577. Bower, "Osmunda and Todea," *Q.J. Micro. Sci.*, xxv., 1885. "Meristems of Ferns," *Ann. of Bot.*, iii., 1889. *Land Flora*, chap. xiv., 1908. Conard, "Hay-scented Fern," Carnegie Inst., Washington, 1908. Campbell, *Mosses and Ferns*, 1918, where full citation is given. Von Goebel, *Organographie*, 1930, *passim*. (*Vascular Anatomy*): A full citation of literature up to 1925 is given in *Ferns*, vol. i., pp. 192-4, referring to its chaps. vii, viii and x. The following is a selection brought up to date: De Bary, *Comp. Anat.*, Engl. edn., 1884. Van Tieghem, "Polystélie," *Ann. Sci. Nat. Bot.*, 1886. Schoute, *Stelärtheorie*, Jena, 1903. Tansley, "Fil. Vasc. Syst., *New Phyt.*", Reprint, 1908. Campbell, *Eusp. Ferns*, Carn. Inst., 140, 1911. Charles, "Marattia," *Bot. Gaz.*, li., 1911. Sinnott, "Leaf-trace," *Ann. of Bot.*, xxv., 1911. Bower, "Medullation," *Ann. of Bot.*, xxv., 1911. Benson, "Botryopt. antiqua," *Ann. of Bot.*, xxv., 1911. P. Bertrand, "Anat. Fougères anciennes," *Progr. Rei. Bot.*, iv., 1912, p. 182. Davie, "Pinna-trace," *Trans. R.S. Edin.*, vol. i., 1914; vol. lii., 1917. *Ann. of Bot.*, xxxii., p. 233. McLean Thompson, "Six Memoirs on Fern Anatomy," *Trans. R.S. Edin.*, 1915-1922. Bancroft, "Rachiopt. cylind.", *Ann. of Bot.*, xxix., 1915. Schoute, "Stele of Marattiaceae," *Trav. Bot. Néerland.*, xxiii., 1926. Holden, "Ankyr. corr.," *Phil. Trans.*, B, vol. 218, 1932. Godwin, "Cyathea," *New Phyt.*, xxxi., 1932. Also Bower, *Size and Form*, 1930, chaps. vi-viii. Sahni, "Zygopteris primaria," *Phil. Trans.*, B, vol. 222, 1932, p. 29.

Such results give confidence in the seriation, though we trace it at the outset in so detailed a feature as apical segmentation.

Since most students become acquainted first with the details of the Leptosporangiate Ferns it will be well to start from these, though fully conscious that their segmentation is more highly specialised than that of the Eusporangiates. Their axis is terminated by a slightly conical tip, at

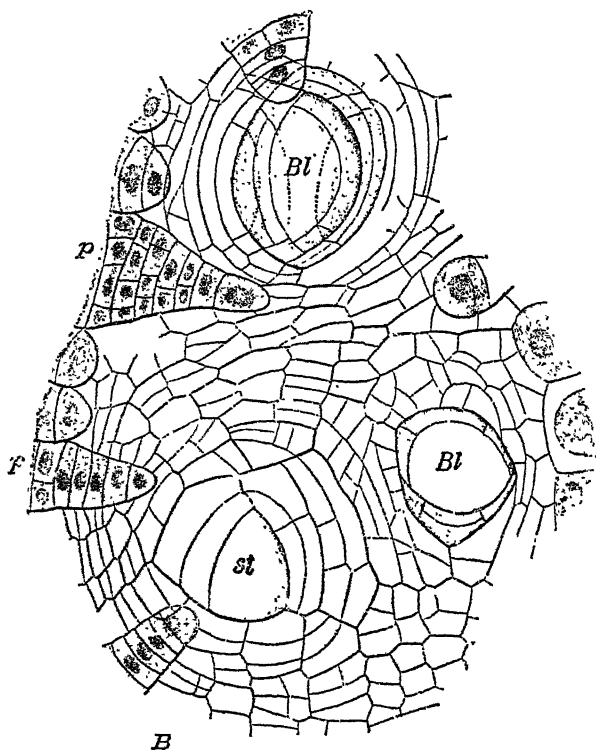


FIG. 255.

Apical view of the growing stem-apex of *Polypodium vulgare*, with its three-sided conical initial cell (*st*), and two young leaves (*Bl*) with two-sided initials; also numerous young ramets are seen (*p*, *p*). (After Klein.) $\times 280$.

the distal centre of which there is a single initial cell. In form it is usually a three-sided pyramid, the base of which is part of the outer surface of the plant, its apex being directed inwards. From the three slightly convex sides segments are cut off in regular succession by walls parallel to them: consequently the fourth segment will be opposite to the first, and so on (Fig. 255). Such development is slow, and it is stated that in certain instances only a few segments are formed in each year. Creeping rhizomes such as that of the Bracken may have a two-sided initial cell, but this is exceptional. In either case a vertical section discloses the pyramidal form of the initial,

and the relation of its segments to the tissues that are developing onwards to the adult state. A three-sided pyramid is also found at the root-tip, but with the additional complication that after each series of three lateral segments a fourth is cut off from the base to form a layer of root-cap (Fig. 256,

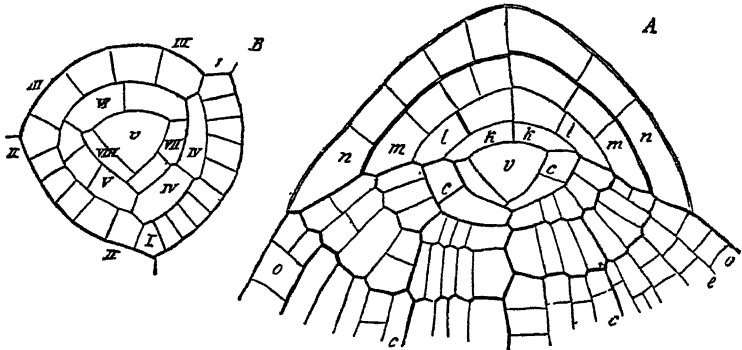


FIG. 256.

A, Longitudinal section through apex of the root of *Pteris*. B, Transverse section through the apical cell of the root, and neighbouring segments of *Athyrium* (after Naegeli and Leitgeb). *v*=apical cell; *k, l, m, n*, successive layers of the root-cap; *o*, dermatogen; *c*, limit of the stele. (From Sachs.)

k, k). Each leaf in the typical Leptosporangiate Ferns arises from a single superficial cell of the axis in which, after a few irregular cleavages, a two-sided initial is established; one of its edges is directed to the centre of the apical cone, the other away from it, while the segments cut off from it form two rows, right and left (Fig. 255 B1). In most Ferns the leaf is a winged structure, with lateral flaps originating from the regular and repeated segmentation of cells occupying the margins; these arise from the middle region of each successive segment of the apical cell itself (Fig. 257). The marginal cells undergo regularly alternating cleavages, which contribute respectively to the upper and lower surfaces of each lateral flap. Thus the leaf-expanse is built up from the products of two layers of segments derived from the marginal cells

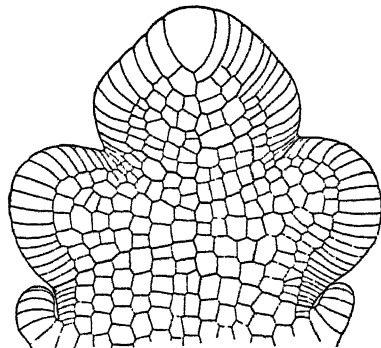


FIG. 257.

Young leaf of *Ceratopteris*, in surface view, after Kny, showing two-sided, apical cell, and the marginal series continuous round the young pinnae. The latter do not correspond individually to the segments from the apical wall.

(Fig. 258). From such illustrations we may conclude that definite segmentation of a single initial cell is characteristic for the primary meristems that give rise to the vegetative organs of the Leptosporangiate Ferns. Finally, the leading feature which characterises the Leptosporangiate

Ferns as distinct from the Eusporangiate is that in them each sporangium also springs from a single cell, which grows out from the surface-tissue, and undergoes regular cleavages presenting a certain analogy with those of the initial cells (Fig. 259, *a*). These will be described in detail later. Meanwhile the interest lies in the delicacy of the unicellular origin, and the correspondence of the cleavages in the young sporangium to those of the vegetative organs. Such segmentation is prefigured by the first cleavages of the embryo, and it may be held as a fundamental character of these more specialised Ferns.

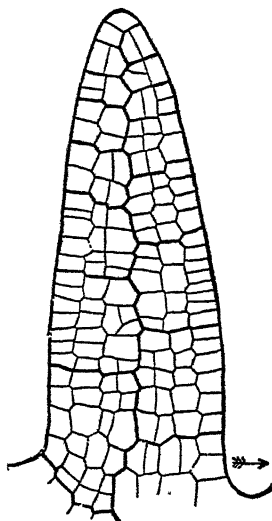


FIG. 258.

Usual type of segmentation at the margin of the leaves of Leptosporangiate Ferns, as seen in *Scolopendrium vulgare*. The arrow indicates adaxial direction.

Fig. 260. Here there is no single initial: in its place there are four initials (marked *x*), or sometimes three; they are of deep prismatic or conical

Passing to the Eusporangiate Ferns, in which the sporangia as well as all the other parts are more massive, each sporangium is referable in origin not to a single cell but to the common outgrowth of a group of cells (Fig. 259, *g*). An examination of the meristems of an adult plant shows that this more complex state is also a common though not a constant character for their vegetative parts. The apical meristem of the adult axis in *Angiopteris* is shown in

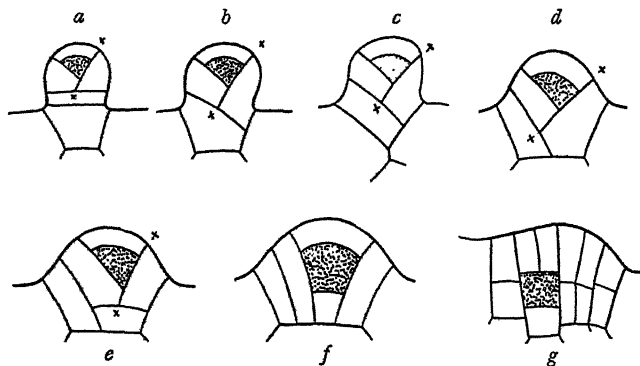


FIG. 259.

Diagrams illustrating the segmentation of Ferns. *a*=Polypodiaceae. *b*=*Ceratopteris*. *c*=*Alsophila*. *d*=*Schizaea* or *Thyrsopteris* or *Trichomanes*. *e*, *f*=*Tokea*. *g*=*Angiopteris*.

form. In the leaves of fully grown plants the apex is similarly constructed but in young leaves, and particularly in *Marattia*, there may be only a single pyramidal cell, though of smaller relative size and less regular

segmentation than in the Leptosporangiateae. The wings of the leaf in *Angiopteris* are also relatively massive, and in section they show a complex segmentation without any definite marginal series; in fact their structure has a quite different appearance from that of the Leptosporangiateae, and is similar in plan to that of a young sporangium as seen in median section (Fig. 261, *A*). The root is, however, the most distinctive part in this respect. As first shown by Schwendener (*Sitz. K. Preuss. Akad. Wiss.*, 1882) the massive roots of the Marattiaceae have, as a rule though not without exceptions, four truncated prismatic initials, a structure which is found sometimes quite diagrammatically also in the Osmundaceae (Fig. 262). The origin of the lateral roots from the main root has been traced in *Angiopteris*, and it is found that the four initials are established by the first segmentations from the single rhizogenic-cell of the endodermis (Fig. 263, *A, B, C*): this shows how deeply that type is established in its organisation; nevertheless in sporeling roots a single initial may be found. The Ophioglossaceae, and

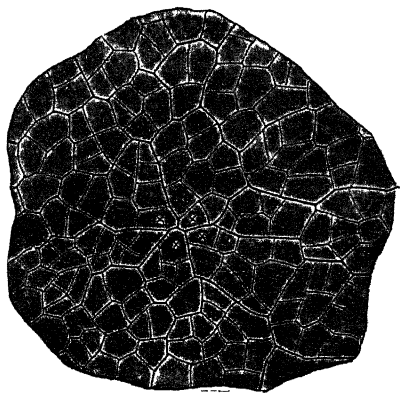


FIG. 260.
Apex of stem of *Angiopteris evecta*, seen from above.
Apparently there are four initials (*x, x*). $\times 83$.

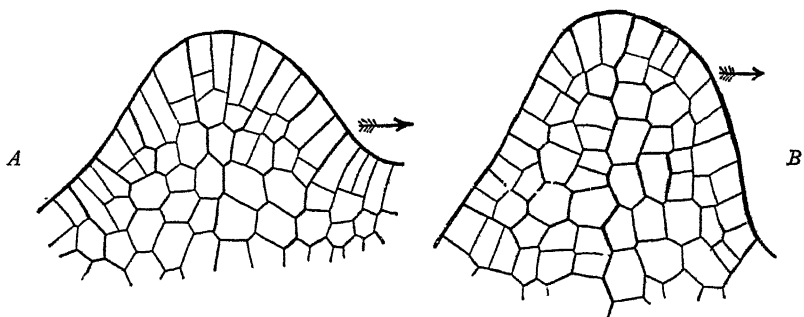


FIG. 261.
Vertical sections through the massive wings of the leaves of *Angiopteris* (*A*), and of *Todea barbara* (*B*). The arrows indicate adaxial direction.

in particular the Osmundaceae, take a middle position in respect of segmentation. In the latter the stem has a three-sided initial (*Living Plant*, Fig. 383). The leaf also has the same, in sharp distinction from that of the Leptosporangiate Ferns, where it is regularly two-sided (Fig. 264). (Compare Figs. 255, 257.) The wing of the leaf of *Osmunda* is massive and, as in the Marattiaceae, there is no definite marginal series of cells (Fig. 261, *B*). The

root also fluctuates between the Leptosporangiate type and the segmentation seen in *Angiopteris*; but the largest roots conform to the type with four

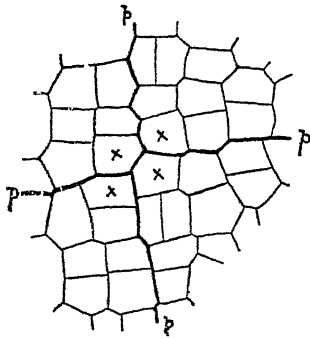


FIG. 262.

Transverse section through the root-tip of *Todea barbara*, showing four initials (x), and the principal walls (p, p). $\times 200$.

prismatic initials (Fig. 262). Such being the condition of the vegetative organs it is natural to expect an intermediate state in the sporangia of the Osmundaceae. Here they are relatively large, and in *Todea* the types of segmentation seen in Fig. 259, e, f, were derived from the same leaf: the one corresponding to the Leptosporangiate type, the other to the Eusporangiate. For further details reference should be made to special memoirs. (Bower, *Ferns*, where the literature is fully quoted.)

The facts here briefly stated show that two types of segmentation exist, and that the one or the other is generally characteristic

for all the adult organs. The one type with a plurality of initials of prismatic form occurs in typical Eusporangiates; the other with a single initial of conical form in the typical Leptosporangiates. The former is prevalent in the more primitive and robust, the latter in the later and derivative Ferns. But there is abundant evidence of transition between these two types of organisation. Increased precision in segmentation accompanies the finer texture of the Leptosporangiatæ: and mere individual size will not wholly account for

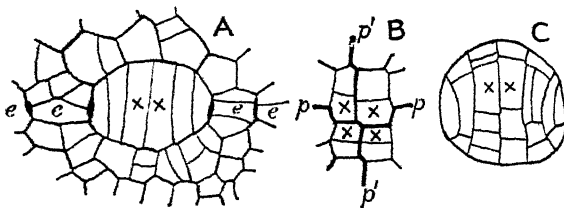


FIG. 263.

Angiopteris evecta: origin of lateral root from a single cell of the endodermis: A, C, transverse through the parent root, showing group of cells forming a new lateral root, with initials already defined by segmentation. B, transverse through the tip of the lateral root, still within the cortex. x, x, the initial cells. p, p, principal walls. $\times 144$.

the differences seen. It is a question rather of inner organisation, which has progressed in refinement from the Palaeozoic Period to the present day; the Eusporangiate state, with its more complex but less precise cleavages, was the prior type. This is not the place to discuss fully the problem of what it is that determines the regular methods of segmentation so beautifully illustrated in the apices of Ferns. For us here the point is that their differences may be used in broad comparison.

There is no obligatory correspondence between segmentation and the genesis of parts or of tissues in Ferns. It is true that there may be such correspondence; for instance, Kny has clearly shown how in *Ceratopteris* one leaf springs from each segment of the apical cell (*Parkeriaceae*, Dresden, 1875, plate xxii.); and Klein has stated that one leaf is produced from each of the two dorsal segments of the rhizome of *Polypodium vulgare*, though none arises from the ventral segments; moreover, in many Ferns the subdivision of the segments at the root-tip accords accurately with the limits of the stele. But against such facts must be set the absence of correspondence between the segmentation of the leaf-apex and the origin of pinnae in *Ceratopteris* itself (Fig. 257); also the further fact that while in most Leptosporangiate Ferns the wings of the leaf arise from the middle region of each segment, in the Osmundaceae each wing arises from the marginal regions of two of the three rows of segments (Fig. 264). Lastly, as we shall see later, in ordinary Leptosporangiate Ferns three lateral segments are cut off from the sporangial mother-cell; but in *Metaxya*, *Cyathea*, and some others there are only

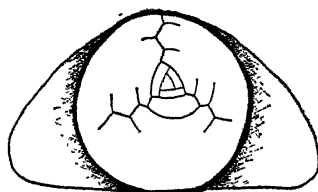


FIG. 264.

Apex of leaf of *Osmunda*, showing the three-sided apical cell in its relation to the two latest pinnae. $\times 26$.

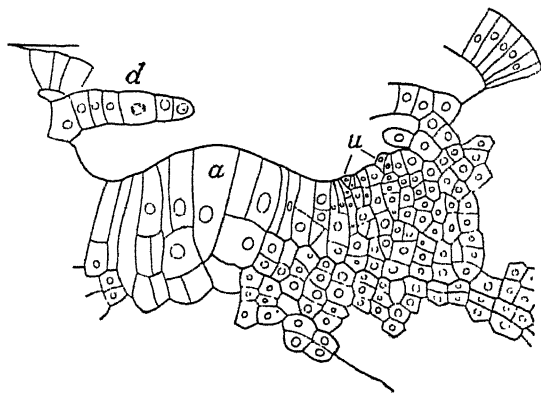


FIG. 265.

Longitudinal section of the stem-apex of *Dennstaedtia punctilobula*, after Conard. The heavy lines on the right show the boundary of the stelar tract. *d*=intercalary growth of hair. *u*=origin of hairs. $\times 110$.

two, and yet the orientation of the annulus remains the same in them all (*Ferns*, vol. ii., Figs. 555, 566). Such examples show that a correspondence between segmentation and the origin of adult structural features may exist, but that the two do not stand in obligatory or constant relation.

Evidence as regards the segmentational origin of internal tissue-tracts is not fully to hand for Ferns. In monostelic types naturally the central

stele originates from the inmost part of the successive segments. In certain solenostelic types, however, the steles are not formed from the inmost of the three parts into which each segment divides, but from the middle one, the outer forming the cortex and the inmost the parenchymatous tract usually called pith. This has been demonstrated for *Dennstaedtia* by Conard (Fig. 265). Such facts accord with the general statement of Schoute, that the correspondence between the meristematic layers of Hanstein and the primary tissues of Van Tieghem holds in some few cases where Hanstein's tissue-tracts are clearly defined, but not always (*Die Stelär-Theorie*, 1902, p. 163). Hence, whether we are tracing the origin of parts defined externally or of the internal tissue-tracts, their genesis appears to be independent causally of segmentation, notwithstanding that the two may at times coincide.

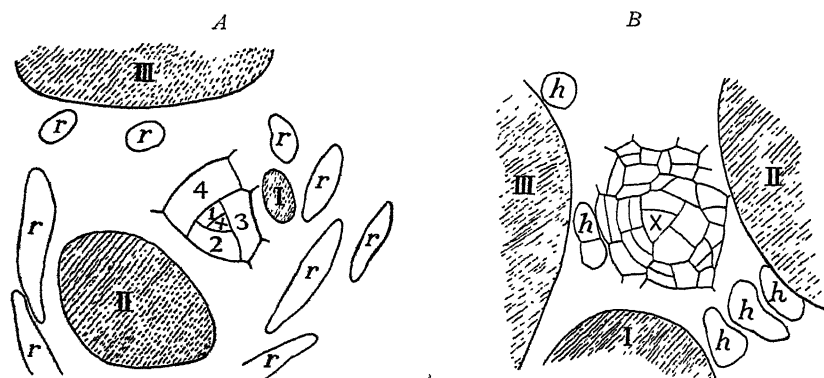


FIG. 265 bis.

Semi-diagrammatic traces taken from photographs supplied by Dr. Lang, but with the segmentation accurately drawn; they show transverse sections of the apex of the shoot: *A*, of *Dryopteris Filix-mas*. *B*, of *Osmunda regalis*. In both there is an antidromous relation of the apical segmentation to the succession of the cladode leaves, which are shaded. *h*=hairs; *r*=ramenta. *A* \times 125; *B* \times 200.

We thus conclude that on the one hand apical segmentation, and on the other morphological definition whether external or internal, are distinct processes, each of which is determined by the apical region as a whole, and not by its segments.¹

A striking demonstration that the origin of cladode-leaves in Ferns is independent of the apical segmentation has recently been given by Dr. Lang. His photographs confirm the statement of Schwendener that the spiral succession of Fern-leaves may be antidromous to the successive cleavages in the growing point that produces them. Nevertheless in other examples it may be homodromous. Transverse sections were cut showing the plan of the apical cone, and of the leaf-succession in *Osmunda regalis*, and in *Dryopteris Filix-mas*. In both of them instances of antidromous succession of leaves have been seen. The sections of the apex of *Dryopteris* also illustrate the irregular disposition

¹ For a more full account of apical segmentation see *Ferns*, vol. i., chap. vi., where the literature is quoted.

of the rammenta relatively either to the leaves, or to the apical cleavages (Fig. 265, *bis*, *A*, *B*). Thus segmentation and organogeny are proved to be two independent propositions; they may in some instances actually coincide: each segment may produce a leaf, as it does in the formation of the leaves of Mosses, or in that of the leaves of *Ceratopteris*. But in general there is no obligatory relation between the two events. The whole position, whether for external or for internal morphology, has been well summed up, from the zoological side, by Whitman in the statement that the organism dominates cell-formation—" . . . massing its material and directing its movements as if cells did not exist " (*Journ. of Morphology*, viii., 1893, p. 653). On the Botanical side De Bary has formulated his view in an aphorism: " Die Pflanze bildet Zellen, nicht die Zelle bildet Pflanzen " (D'Arcy Thompson, *Growth and Form*, 1917, p. 200). This conclusion will apply equally for the apical meristems of the adult plant, and for the initial steps of organogeny in the embryo.

VASCULAR SYSTEM. A. STEM

Passing to the comparison of adult tissues, it is to the conducting system that we naturally turn. The tissues that embed it are so variable in their character that they are less trustworthy as evidence than the stable vascular tracts; while the latter preserve their features better under fossilisation. On both grounds the weight of comparison falls upon the vascular system.

The Microphyllous Pteridophytes were designated by Jeffrey the *Lycopsida*, and diagnosed by him anatomically by the absence of foliar gaps in their vascular system ("Cladosiphonic"). The Megaphyllous Pteridophytes, styled by him *Pteropsida*, were distinguished as possessing foliar gaps ("Phyllosiphonic"). The names *Lycopsida* and *Pteropsida* have been widely adopted, and have passed into general use; but the anatomical distinction is open to so many significant exceptions that it is practically valueless. The existence of a foliar gap as a structural feature does not depend upon or indicate phyletic origin, but connotes a size-relation of the leaf to the axis which bears it. This may work out as a disturbance of the axial structure at the departure of the trace to relatively large leaves of advanced types; but a foliar gap is naturally absent from all protostelic Ferns, and from the sporelings of those in which gaps may appear in the adult. It is in fact a phenomenon of balance of appendage to axis, which may be expected to produce its structural result in megaphyllous rather than in microphyllous types, though inherently characteristic of neither. It is necessary to state this at the outset, so as to make the position clear; for certain primitive examples of "*Pteropsida*" will be first described which have no foliar gaps, even in the adult. (See p. 332.)

The Filicales with very few exceptions are without cambial thickening; but many of them show, in compensation for this, a high degree of elaboration of the primary vascular tissues of the stem. These, however elaborate, may all be referred in origin to the *monostele*, which is the starting point

not only in Descent as shown by comparison of early fossils, but it also appears in the ontogeny of each individual. The form of the stem itself is obconical, as already explained (compare Figs. 225 and 266). If transverse sections cut at various levels are drawn to scale the result in a given case comes out as in Fig. 266. Here not only is the great increase in size evident, but with it goes a progressive increase in elaboration of the primary conducting tracts, whether of stem or of leaf. The minute stem of the sporophyte

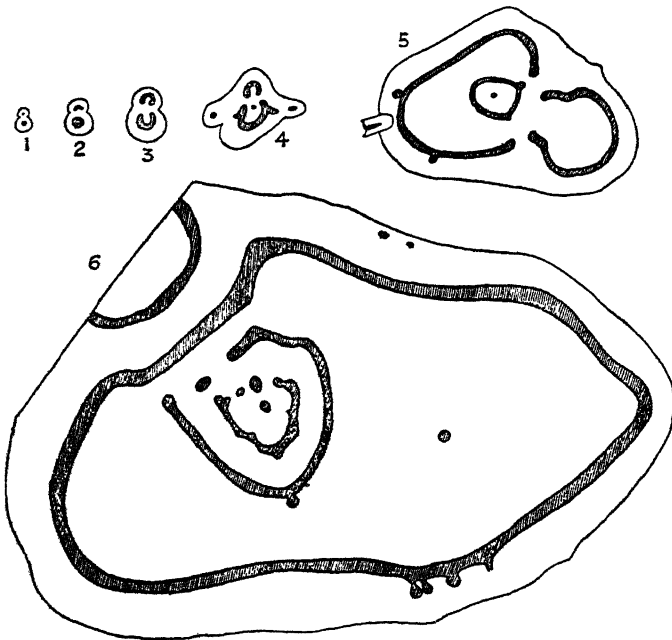


FIG. 266.

Series of transverse sections of the stem of *Pteris* (*Litobrochia*) *podophylla*. All are drawn to the same scale, and show the great increase of stelar complexity as the conical stem expands upwards. $\times 4$.

of *Pteris podophylla* is traversed by a simple protostele with the leaf-trace a simple conducting strand (1, 2); but the adult stem contains a highly elaborated system of concentric rings (5, 6), while the leaf-trace is a wide horse-shoe or even a closed ring. The elaboration of the structural scheme may be held as a set-off to the absence of cambial thickening, in providing a means of meeting the increasing demands for transit in an enlarging shoot. This method holds for all modern Ferns.

The dependence of the Filicales upon elaboration of the primary conducting tracts rather than on cambial increase is all the more remarkable since many primitive Pteridophytes, such as the Lepidodendroids and Calamarians, possess secondary thickening. Even within the Filicales it has had a sporadic hold among the Zygopterids. Tentative examples have been recorded in

Metaclepsydropsis (Gordon), and in *Ankyropteris corrugata* (Holden). But the best known instance is that of *Botrychioxylon* described by Scott, which may perhaps have been identical with *Zygopteris primaria* Cotta (Sahni). Here the secondary development was normal, and apparently constant in the stem, and it has been observed also at the leaf-base, and in the root. "The prevalence of secondary xylem, and especially the complete replacement of primary by secondary tissue in the outer zone of wood in the stem, is the main feature of the genus: there is here a manifest analogy with *Botrychium* among the Ophioglossaceae; anatomically *Botrychioxylon* stands in the same relation to the typical Zygopterid as *Botrychium* to *Ophioglossum*" (Scott, *Studies*, i., pp. 321-2; Sahni, *Phil. Trans.*, July 1932). The replacement of primary by secondary xylem is seen to be as effective in large stems of the living *Botrychium virginianum* as it is in a Dicotyledon. The primary wood is represented only by a meagre and interrupted circle of tracheides surrounding the large central pith; while the cambial wood, vitalised by numerous medullary rays, forms the greater part of the effective xylem (*Ferns*, i., Fig. 129; ii., Fig. 349). Steps leading towards this state have been traced in *B. Lunaria*, from the solid tracheidal core of the sporeling, through medullation, and a rudimentary cambial activity (Bower, "Medullation," *Ann. of Bot.*, xxv., 1911). Thus in ancient Zygopterid fossils, as well as in the modern *Botrychium*, cambial thickening has taken hold. But neither the fossils nor the living Ferns seem to have ever used the opportunity which it offered to the full. Modern Ferns have clung to primary development with all its disabilities; but thereby they have presented a striking example of a rear-guard physiological fight against the inevitable consequences of increasing size, by high elaboration of form of the primary conducting tract.

A reason for the high elaboration of form instead of direct enlargement without change of form may be explained thus: according to the Principle of Similarity, as the size increases the surface will increase only as the square of the linear dimensions, but the bulk will increase as the cube. Consequently the proportion of presentation-surface to the bulk of the conducting tract would be constantly diminishing if the form remained the same during enlargement, and risk of inefficiency of the conducting and distributing tissue through lack of presentation-area would follow. Any change of form from the original cylinder would tend to meet this difficulty, hence there is a functional reason for the increasing elaboration of form of the primary tissues as seen in Ferns. In particular the dead tracheidal tissue offers a surface of transit of material to and from the living cells which embed it. Where the wood consists of tracheides only, as is its state in most of the primitive plants, the collective surface of the whole woody tract deserves special attention from this point of view. The more elaborate its form the greater the proportion of surface for transit will be, and the greater the efficiency for distribution between the dead conduits and the living tissues. That surface is perhaps the most important of all: certainly it is more liable to elaboration than that of the endodermis, which delimits the conducting tracts from the surrounding tissues; and still more so than the external surface, which is usually unaltered by the changes within. Such considerations, which have been more specifically stated elsewhere, provide a working hypothesis which will give added interest to the study of the

very elaborate primary conducting tracts of Ferns. A series of examples, some taken from early fossils, others from Ferns now living, will serve to show the various ways in which the problem has been actually worked out in nature (Bower, *Size and Form*, Macmillan, 1930. See also below, Chapters XXVIII and XXX, where this subject will be more fully considered).

An early example of the protostele in Ferns is provided by the adult stem of the Carboniferous fossil *Botryopteris cylindrica* (Fig. 267). The

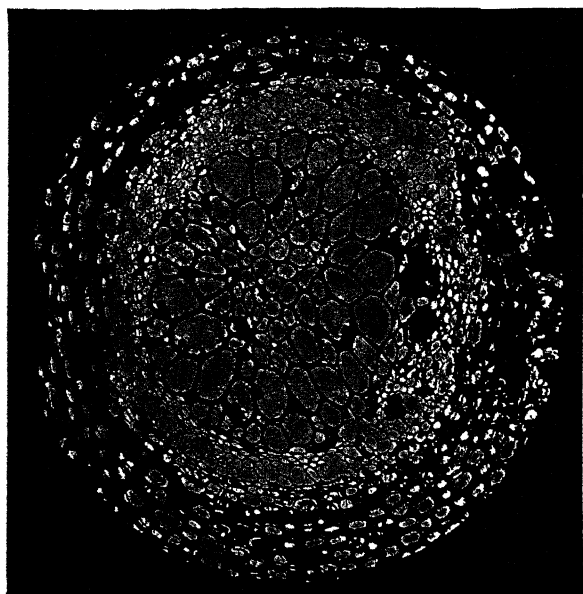


FIG. 267.

Transverse section of a stele of *Botryopteris cylindrica*, showing a protostele with a solid core of xylem, and peripheral phloem. The endodermis is not clearly shown in this fossil Fern.

stele is small and cylindrical, the diameter of its very perfect sectional circle being considerably under 1 mm. It is composed of a central solid core of tracheides, the smallest of these near to the centre being the protoxylem: this is surrounded by a broad band of well-preserved phloem, but the external sheaths are not clearly defined. Other fossil Ferns are also protostelic, and those of larger size illustrate one of the methods by which the consequent difficulties, explained in the foregoing small-type paragraph, are met. The perfectly cylindrical form is not retained, but the stele is fluted, presenting according to size a more or less deeply stellate outline, as seen in transverse section. For instance, in *Ankyropteris Grayi*, where the stele may be 2-3 mm. in diameter, hollows of varying depth lie between the projecting insertions of the leaf-traces, their depth being related to the size of the individual (Fig. 268, 2, 3). A more extreme instance of this fluting is seen in the large

stele of *Asterochlaena laxa*, which may be as much as 15 mm. in diameter (4). In this Fern the stem was probably upright, and numerous relatively small leaves are inserted upon it. The stele is deeply furrowed, but the number and position of the flanges bear no constant relation to that of the leaf-traces; thus the moulding of the flanges is not a consequence of leaf-insertion. In this *Asterochlaena* resembles the adult shoots of *Lycopodium*,

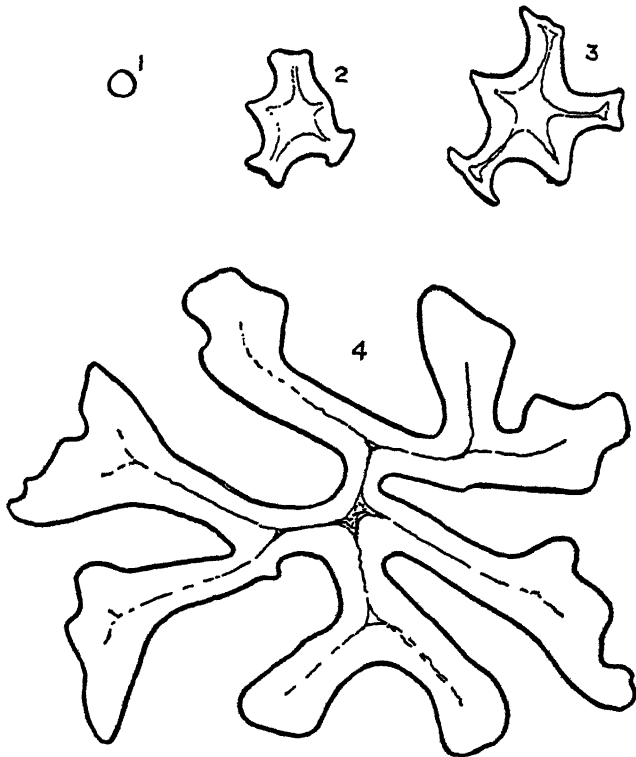


FIG. 268.

Outlines of the xylem of Coenopterid steles, all drawn to the same scale, to show their relative sizes ($\times 5$). 1=*Botryopteris cylindrica*. 2=*Ankyropteris Grayi*. 3=ditto, larger. 4=*Asterochlaena laxa*. The elaborateness of outline increases with the size.

as already explained (p. 221-2). Such facts, shared by plants systematically so distinct, support the view that the fluting is a feature of the stele itself, adaptive according to size.

In certain Ferns the protostelic state is maintained throughout life. This was so in *Botryopteris cylindrica* and other fossils. It is found also in many living Ferns: such as *Gleichenia*, *Lygodium*, *Cheiropleuria*, and in the whole family of the Hymenophyllaceae. Some biological explanation may be found for this retention of the juvenile state in the fact that the Ferns named are rhizomatous, with thin leaf-stalks containing a contracted vascular

strand. The stele of a creeping stem which is not specialised for storage is not thus influenced towards expansion by mechanical claims, nor yet by the insertion of crowded or broad-based leaves. Modern types, however, which retain the protosteles possess a structural feature which is either absent or imperfectly developed in those that are more primitive: viz., the presence of living parenchyma interspersed among the dead tracheides (Fig. 269). This is in strong contrast to the purely tracheidal wood of such ancient but extinct plants as *Thamnopteris* and *Asteroxylon*, and most species of *Lepidodendron*. *The facts suggest that purely tracheidal wood does not*

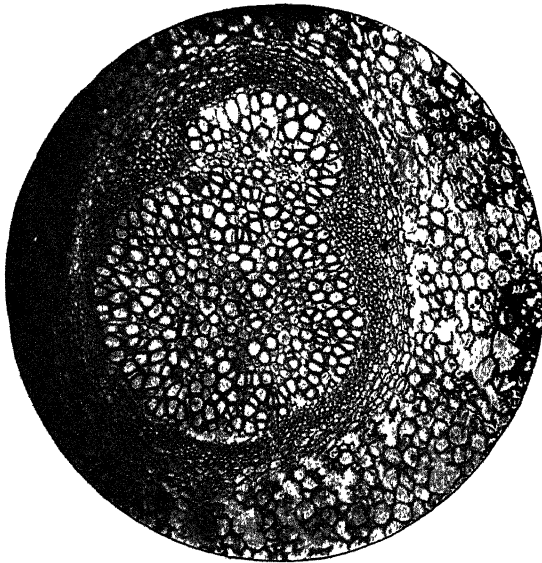


FIG. 269.

Transverse section of a protostele of *Chetropleuria*, showing a leaf-trace being given off from it. ($\times 45$) Parenchyma is present scattered through the central region of the wood.

possess survival value to-day except in small strands. A remedy seems to have been found in the presence of scattered living cells which *vitalise* the wood. Their presence tends to increase the sum of presentation-surface of the dead tracheides, and so to solve the chief functional difficulty presented by increasing size. Most protosteles of living Ferns are nevertheless small, with a xylic core ranging in the adult from .7 mm. to 1.0 mm. Even *Gleichenia Montaguei*, which has the largest protostele observed in any living Fern, and probably of any living vascular plant, has a xylic core only 3.0 mm. in diameter. But provided the wood be permeated, as it is in this Fern, with living cells, there is no reason why still larger protosteles should not exist. In the past they certainly have—for example, *Sutcliffia insignis*, with a stelar diameter of over 3.0 cm.; but its wood is very thoroughly vitalised (Scott, *Studies*, ii., p. 201. Bower, *Size and Form*, chap. ix.).

Living cells are found to have been present within the wood of certain early fossils, particularly where the size is considerable: it is a state related to the initiation of pith. The central region of the large xyletic tract of *Asterochlaena*, as also of the smaller in *Ankyropteris*, consists of wide short tracheides and parenchyma. This feature, which has been described as a "mixed pith," is present also in other fossil Ferns such as *Metaclepsydropsis*,

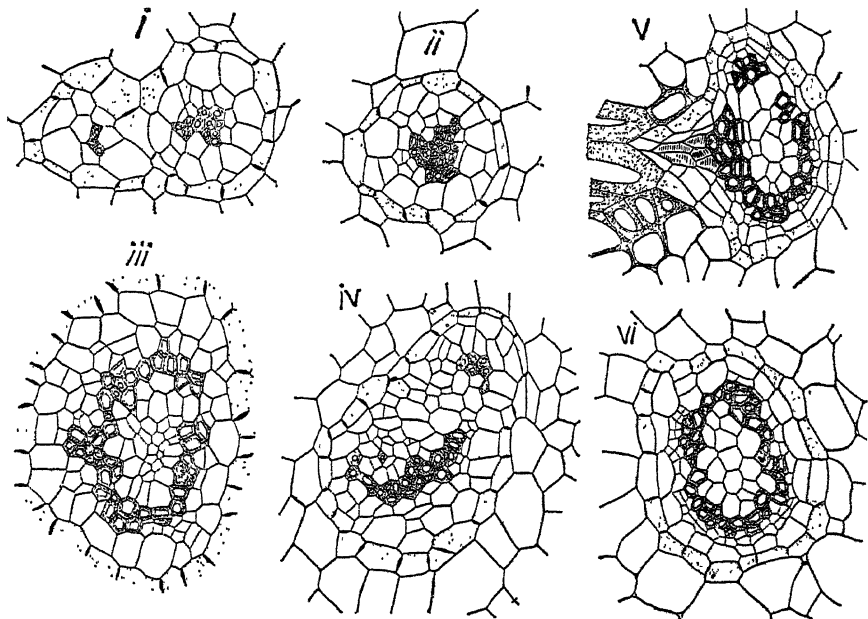


FIG. 270.

Transverse sections, in succession from below, of the axis of a young plant of *Anemia*. *i*, proto-stele gives off leaf-trace without any interruption of the endodermis; *ii*, proto-stele higher up; *iii*, still higher, with central pith; *iv*, same stele giving off a leaf-trace without interruption of the endodermis: note isolated tracheid in the pith; *v*, *vi*, transverse sections of adult stele of *Schizaea rupestris*; *vi*, shows a continuous xylem round central pith; *v*, shows departure of a leaf-trace; to the left a root-trace. The endodermis is dotted. $\times 150$.

and in some of the fossil Osmundaceae: it may be held as a state transitional towards medullation. In a more advanced stage it appears also in primitive living Ferns, such as *Ophioglossum* and *Botrychium*. Here there is at first a small purely tracheidal tract of xylem; higher up a central region develops as parenchymatous pith, but occasional tracheides lie isolated within it (compare *Ferns*, i., Fig. 119). In *Anemia* and *Schizaea* the ontogenetic stages seen in Fig. 270 mark a like progression, though on a smaller scale, with an initial tract of solid xylem (*i*, *ii*), which soon acquires an internal pith (*iii*), with an occasional included tracheid (*iv*). The whole ontogenetic progression, including the departure of the leaf-trace, is here carried out within a continuous endodermis: hence the pith is clearly intra-stelar. The establishment of a pith thus traced ontogenetically leads

to that structure that is known as *solenoxyllic*. Where the wood, whether vitalised or not, is bulky and the leaf-traces relatively small, the central pith

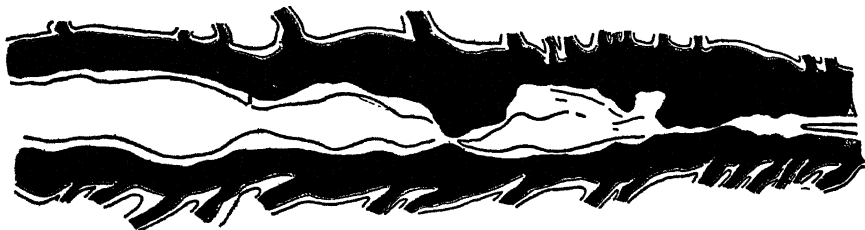


FIG. 271.

Reconstruction from sections of the stele of a small plant of *Platyzoma*. The base is to the right. Outer and inner endoderms represented by black lines; xylem is black. Pericycle, inner parenchyma, and pith are white. The diagram represents the general arrangement of tissues as it would be seen in a median longitudinal section. $\times 10$. (After Dr. J. McL. Thompson.)

may still be completely surrounded by a zone of xylem which is not interrupted by the direct departure of the leaf-traces; in fact they pass off as from a simple protosteles. This is seen in the rhizome of *Platyzoma* (Fig. 271). Steps in the origin of such a state are illustrated by

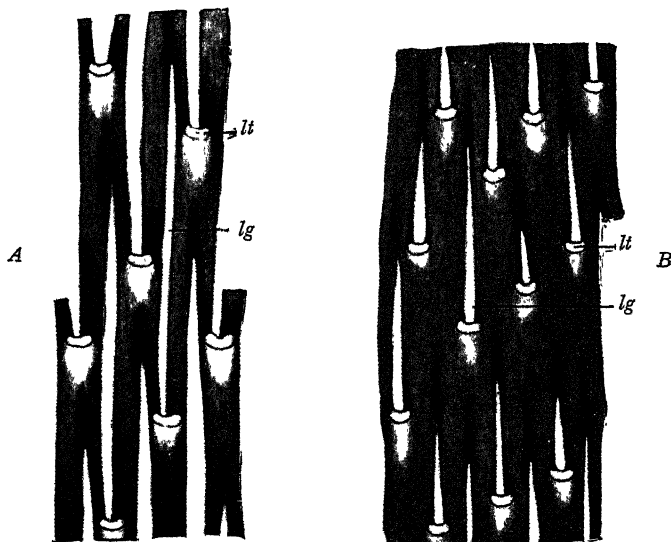


FIG. 272.

A = a representation of a portion of the xylem-ring of *Osmunda regalis* seen from without; *li* = cut end of a departing leaf-trace; *lg* = leap-gap. (After Lachmann, from Kidston and Gwynne-Vaughan.) B = a representation of a portion of the xylem-ring of *Todea barbara*, seen from without. Lettering as above. (After Seward and Ford, from Kidston and Gwynne-Vaughan.)

the Permian fossils, *Grammatopteris* (Sahni, *Ann. of Bot.*, xlv., 1932, p. 863), *Zaleskya*, *Thamnopteris*, and *Osmundites Dunlopi*, which, taken in sequence as named, suggest a progressive establishment of a central pith

in a large protostele with a continuous xylic ring. It is only when that ring is relatively thin and the leaf-traces relatively large that the xylic tract is interrupted at their departure. But then a sector of the ring passes bodily out into the foliar strand, leaving a gap; and if these gaps overlap owing to close arrangement of the leaves the result is that seen in the living *Osmundaceae* and in some related fossils: their state may be described as *dictyoxyllic* (Fig. 272). Accordingly medullation may be recognised as a step towards the states known as *solenostely* and *dictyostely*, which underlie all the more elaborate stelar types in Ferns. But there are still wanting the zones of phloem and of endodermis which line the xylic ring internally in



FIG. 273.

Stele of a full-grown stem of *Osmunda cinnamomea*, from a photograph by Gwynne-Vaughan. $\times 25$.

typical examples of solenostelic structure. A number of instances have been recorded in primitive Ferns where patches of internal endodermis exist. Lang has described these in *Botrychium*, while in large rhizomes of *Helminthostachys* a complete internal endodermis is sometimes present lining the xylic ring internally; a like state has been described by Thompson in *Platyzoma* (Fig. 271). But the most striking cases are those in some of the modern *Osmundaceae*, where an internal endodermis is present lining the dictyoxyllic ring, as in *Osmunda cinnamomea* and in *Todea hymenophylloides*. In the former species some internal phloem has also been found (Fig. 273). All the Ferns above named are relatively primitive types: none of them shows a typical solenostely. These may provisionally be accepted as tentative steps towards that state, not yet fully attained. But solenostely is clearly advantageous functionally, as is shown by its persistence when once it came to be established in the Leptosporangiate Ferns. This whole

question will be taken up for general discussion in Chapter XXVII. Meanwhile the solenostelic state and the further variants upon it may be briefly described.

In typical examples the solenostele is a cylinder, with both outer and inner surfaces delimited from the tissue that embeds it by a continuous sheath of endodermis. The cylinder is filled by a tract of pith, usually parenchymatous but sometimes sclerotic. The detailed structure of a cylindrical solenostele, or of its derivative dictyostele, is illustrated in transverse section by Fig. 274, which was drawn from one of the meristemes of the Bracken. The

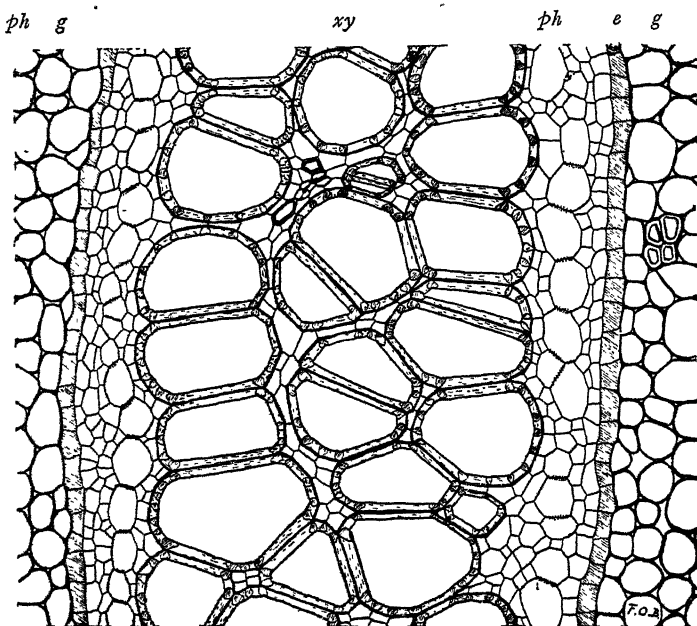


FIG. 274.

Part of a transverse section of a meristeme of Bracken. *g*=ground parenchyma; *e*=endodermis; *ph*=phloem with sieve-tubes; *xy*=xylem with large scalariform tracheids. Some smaller tracheids lying centrally are the protoxylem. Note that no intercellular spaces are seen within the endodermis. $\times 75$.

vascular tissue is shut off from the ground parenchyma (*g*) by a sheath of endodermis (*e*), which forms an unbroken physiological barrier whatever the stelar complications may be. Internally lies a less regular band of pericycle and phloem (*ph*) with large sieve-tubes, while centrally is the xylem (*xy*) consisting of large tracheids, with groups of smaller protoxylem enclosed. The wood is here thoroughly vitalised by parenchyma, so that every tracheid forms contact with living cells at some point of its surface. This is characteristic of advanced Ferns in contrast to those which are primitive, where the wood is usually not so vitalised. In simple rhizomatous Ferns with isolated leaves the cylinder is continuous as an unbroken tube

between the leaf-insertions ; but at these spots a portion of the stelar tube, consisting of a sector of xylem together with attendant phloem and endoder-

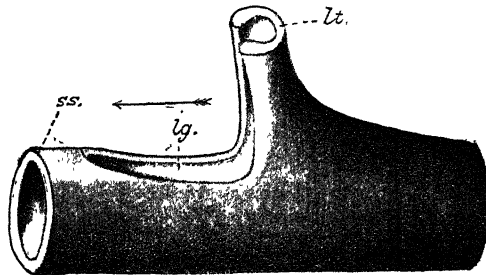


FIG. 275.

Loxsoma Cunninghami. Diagram showing the form of the vascular system at the node of the rhizome. *ss*=solenostele; *lt*=departing leaf-trace; *lg*=leaf-gap. The arrow points toward the apex of the rhizome. (After Gwynne-Vaughan.)

mis, passes into each leaf-base as a *leaf-trace*. This causes a *foliar gap* in the cylinder, through which the pith makes contact with the outer cortex. Notwithstanding this profound disturbance there is no break in the continuity of the endodermal sheath, which throughout envelops both stele

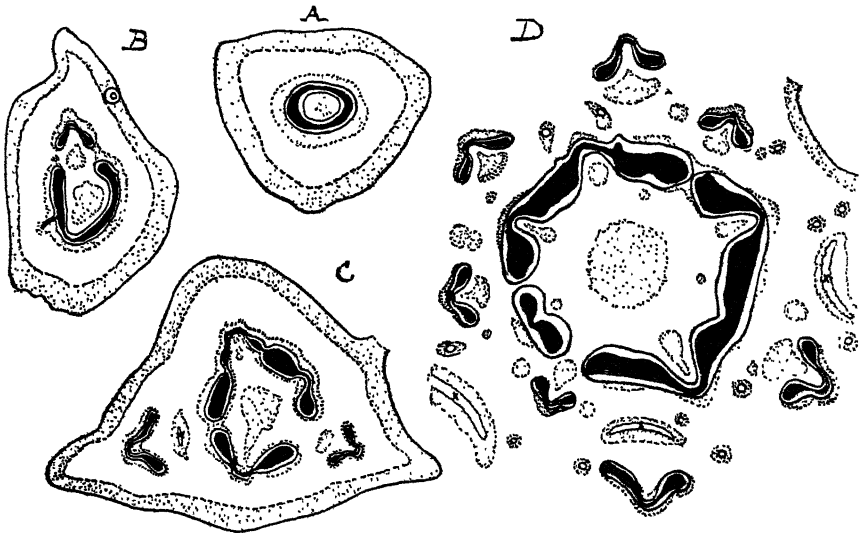


FIG. 276.

Transverse sections of rhizomes of successive ages of *Plagiogyria pycnophylla*, showing transition from solenostely to dictyostely. *A*, solenostelic rhizome; *B*, same giving off a leaf-trace; *C*, larger rhizome with two leaf-gaps; *D*, vascular system of an adult, dictyostelic rhizome: peripheral sclerenchyma omitted. Xylem black, sclerenchyma dotted. (*A*, *B*, *C* $\times 4$; *D* $\times 2$.)

and leaf-trace (Fig. 275). Where the leaves are in close relation to one another the foliar gaps may overlap, and in upright stems with tufted leaves this may cause an apparently high degree of complication. But if its origin

be traced by following the transition from the creeping solenostelic runner with isolated leaves to the upward directed shoot in such a plant as *Plagiogyria*, where the leaf-traces are undivided though crowded, the explanation in terms of departure of meristeles is clear (Fig. 276). Where the leaf-traces are represented, as they are in advanced types, by a plurality of strands each inserted separately on the margin of the foliar gap, the whole structure appears complicated. Nevertheless the stele itself may still be traced in transverse section as a ring of *meristeles*, each separated from its neighbours

by a foliar gap on either side. Thus the original cylinder is still present surrounding the pith, though it is perforated by many overlapping gaps. It is styled a *dictyostele*, since it presents the appearance of a cylindrical network of meristeles (Fig. 277).

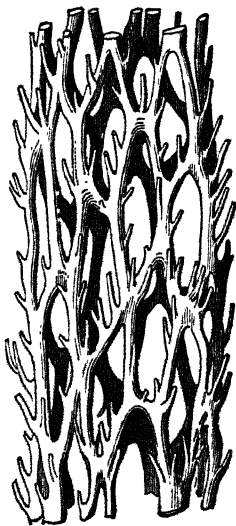


FIG. 277.

Dictyostele of the Male Shield Fern dissected out, showing the overlapping leaf-gaps which allow communication between cortex and pith. (After Reinke.)

The stele itself, whether solenostele or dictyostele, may be dilated to a large size without further complications. Examples of this are seen in *Metaxya* (Fig. 278, 1), with a pith about three-quarters of an inch in diameter; or in *Cibotium Barometz*, of an inch or more; or in *Dicksonia antarctica*, where the pith may measure over three inches in diameter. It is unusual to find such large masses of parenchyma without any conducting system; frequently in other, and even smaller, Ferns the pith is traversed by a medullary system which may take various forms. The most frequent is the appearance of accessory strands or concentric cylinders within the original solenostele or dictyostele, giving the state known as *polycyely* (Fig. 278,

3, 6). Though such developments appear for the most part in relatively large stems, a comparison of them drawn to the same scale shows that a definite relation to size is not obligatory. For instance, while *Dipteris* (2) has a simple solenostele, a rhizome of *Matonia* of about the same size may have three or even four concentric steles (3). On the other hand, the fact that the steles in *Matonia pectinata* make their appearance successively as the elongating rhizome of the sporeling enlarges, is proof that there is a relation to size in the individual (see *Ferns*, i., Fig. 148, p. 154). Moreover, in the smaller species, *M. sarmentosa*, a third ring is not initiated in the slender rhizome, and the second appears to be incompletely formed (*Ferns*, ii., Fig. 499, p. 223). This accords with the facts already shown for *Pteris podophylla*, in Fig. 266, where the complexity increases with the size of the individual. Gwynne-Vaughan's reconstruction for *Pteris elata*

shows in three dimensions the polycyclic structure in a relatively simple example (Fig. 279). Those Ferns in which such accessory developments

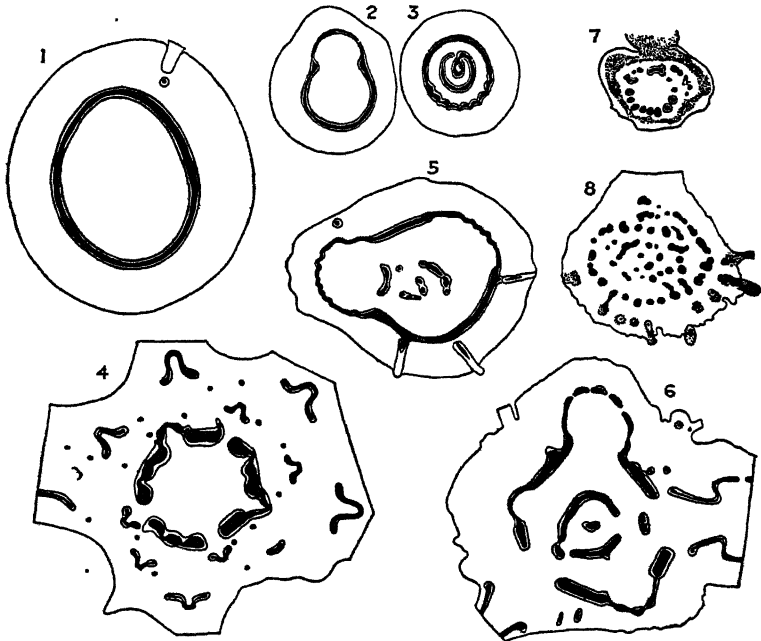


FIG. 278.

A series of solenostelic and dictyostelic stems of Ferns, in transverse section, all drawn to the same scale. ($\times 2$) 1, *Metaxya*; 2, *Dipteris*; 3, *Matonia*; 4, *Plagiogyria*; 5, *Thyrsopteris*; 6, *Saccoloma*; 7, *Platycerium alcorni*; 8, *Platycerium althopicum*. These drawings show that for Ferns at large the disintegration of the stele does not depend on absolute size alone.

are present are not necessarily of near affinity; for instance, *Matonia* (3) and *Platycerium* (8) have no near relation to *Thyrsopteris* (5), *Saccoloma* (6), or *Pteris* (Fig. 266). In these facts there is evidence of a polyphyletic origin of polycyclus.

A further elaboration appears in the *perforation* of the stelar tracts, which is a feature specially present in advanced Leptosporangiate Ferns. It consists in the appearance of gaps in the flattened meristellar tracts, which are structurally like foliar gaps, but they differ in being quite independent of vascular supply to any appendage. They are especially prominent in elongated rhizomes, though they are

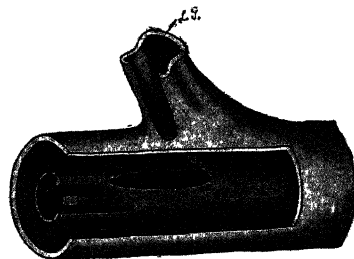


FIG. 279.

Pteris elata, v. *Karsteniana*. Diagram showing the arrangement of the vascular tissue at the insertion of a leaf. A piece is supposed to be cut out of the side of the solenostele, so as to show the internal vascular system. Note that a small strand, lying within the second vascular ring, is also present. (After Gwynne-Vaughan.)

present at times also in upright stocks (Fig. 280). As seen in transverse section, perforations have the effect of breaking up the complex vascular

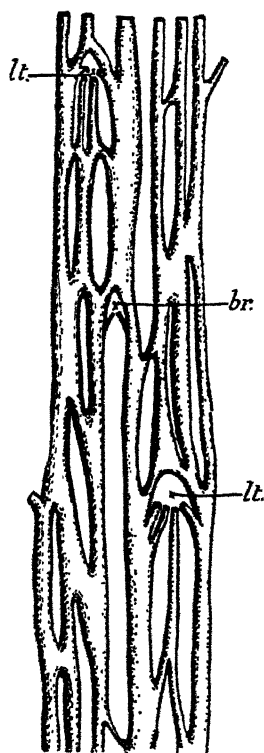


FIG. 280.

Stenochlaena tenuifolia, after Mettenius. Stelar system flattened out into a single plane, showing perforations. *lt.*=leaf-trace; *br.*=vascular supply to a branch.

ring into small isolated tracts (Fig. 278, 7, 8). The sides of each perforation are lined by endodermis which shuts in the vascular tissue completely. Their physiological effect is to offer more free communication between the cortex and the pith than would have been possible if the stelar sheet were unbroken. It will be seen later how important this becomes at the base of the leaf-stalk, especially in large Ferns where there is an otherwise undivided leaf-trace.

This account of the methods of elaboration of the tracts of primary conducting tissue in the Stems of Ferns does not exhaust the subject. The chief features only have been mentioned, by which readjustment of the form is carried out, leading from the simple and often minute protostele to its derivatives, which in large Ferns present a highly complicated plan. The biological aspect of such changes will be the subject of more general treatment in Chapter XXVIII. Meanwhile we may be satisfied here by recognising a general relation of primary structure in Ferns to increasing size and proceed to the examination of the conducting tracts of the leaf from a like point of view.

VASCULAR SYSTEM. B. LEAF

At the close of Chapter XVI the working hypothesis was stated that the megaphyll, together with the axis which bears it, originated from an indifferently dichotomous branch-system. This gives a special interest to the comparison of the foliar meristele with the stele of the stem in the most primitive Ferns. In proportion as the former resembles the latter in plants of known antiquity, so is the support of the working hypothesis which the anatomical comparison affords. We may expect, however, that the bifacial character of leaves should affect the anatomy even of early types. This feature was less pronounced in such plants as *Stauropteris*, and the *Zygopterids*, the leaves of which were upstanding, and even of bushy habit: in

them the vascular meristele is not so markedly dorsiventral as elsewhere (pp. 315-6, Figs. 250, 251). But probably these were not in the direct evolutionary line of the more advanced Ferns. It is in the Botryopterids and the fossil Osmundaceae that the best comparative evidence is to be found, suggesting the origin of the trace characteristic of bifacial leaves as seen in modern Ferns.

Botryopteris cylindrica, from the Lower Coal Measures, is probably the best known shoot of the Botryopterideae: its stele has already been described (Fig. 267). The dichotomous stem in this and other species

gives rise to solitary leaves of which the trace closely resembles the stele of an equal dichotomy, though of smaller size. At its point of origin the

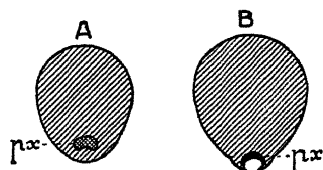


FIG. 281.

Botryopteris antiqua, Kidston. A, foliar trace as it leaves the stem, with an internal pole of protoxylem. B, a foliar trace in the primary petiole, with the pole cup-shaped at the inner boundary. px=protoxylem. (After Bertrand.)

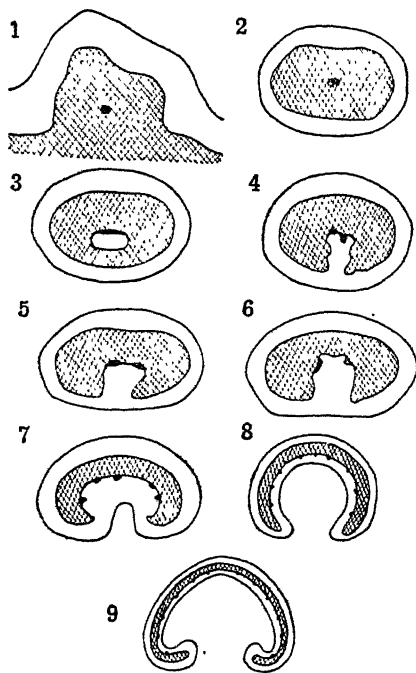


FIG. 282.

Diagrams illustrating the departure of the leaf-trace in *Thamnopteris Schlechtendalii*, Eich. (After Kidston and Gwynne-Vaughan.) These figures are not drawn to a uniform scale; a point which is corrected by Fig. 284.

meristele is oval, with one or two immersed protoxylems (Fig. 431, B, p. 566). As the trace passes into the petiole, the protoxylem moves towards its lower, originally adaxial face, and disintegrates, leading to the tridentate trace of the later Botryopterids. The simplest trace of all is that of *B. antiqua*, from the Petticur Beds, shown in Fig. 281, which, when taken at the very base, links on structurally with what is seen in the simplest Osmundaceous trace. In both the meristele is at first oval in outline of section, with immersed protoxylem: and its opening out into an adaxially curved trace is essentially the same. The steps of advance, as seen in the Osmundaceous fossil *Thamnopteris*, are shown in Fig. 282. The fossil is of Permian age. The figures represent a series of sections of the leaf-trace as seen at successive levels from below upwards. The trace appears first as an outgrowth on the

surface of the xylem of the stem, with a single protoxylem (1); it separates as an elliptical tract of xylem surrounded by phloem and the usual sheaths (2);

an island of parenchyma then appears adaxially to the protoxylem (3), which increases till it opens on the adaxial side (4). The bay of parenchyma then widens, and the protoxylem divides into two (5, 6), and later into numerous groups (7, 8). The outline of the whole trace is at first elliptical, but a surface depression soon appears on the adaxial side: as it widens the trace curves into a broad arch with incurved cusps; meanwhile the xylem thins out and numerous protoxylems are seen along its concave margin (8, 9). It is believed that the stages, thus seen in section, truly indicate the phylogenetic changes involved in forming the leaf-trace of Ferns. But in the more

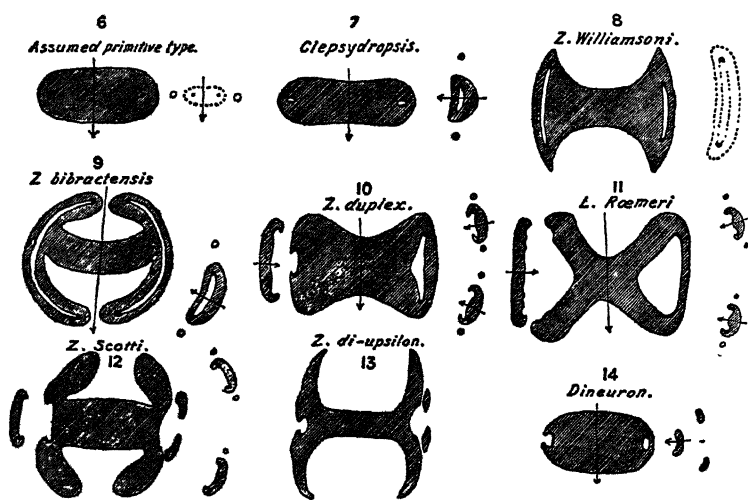


FIG. 283.

Diagrammatic comparison of the various types of Zygopterid leaf-trace. (After Kidston and Gwynne-Vaughan). *Trans. R.S. Edin.*, vol. xlvii, p. 472. The figures are not drawn to the same scale.

advanced types the oval stage at the base is frequently omitted, the trace in ordinary Ferns being curved from the first: this is so conspicuously in the living *Osmunda*, in which, though the later stages accord with 5-9, the trace as first isolated corresponds to Fig. 282, 4. By such steps an anatomical sequence may be followed, partly palaeontological, partly ontogenetic, from a Botryopterid leaf-trace hardly distinguishable from the protostele of the relative axis, to the petiolar meristele of a living though antique type of Fern. Such evidence gives anatomical support for the working hypothesis of 1884. But it was not available till more than a quarter of a century after this was first suggested.

A brief reference may here be made to the complex meristeles of the Zygopterideae, many of which attained very considerable size. There were two types of Zygopterid leaves: first, those with two rows of pinnae, one on each side of the rachis (Clepsydroideae, Sahn); secondly, those with four

rows, two being on either side of it (Dineuroideae, Sahni). The latter appears to have been the result of an early dichotomy of each pinna of the single-rowed type. But knowledge of the upper regions of their leaves is very imperfect, compared with that of the petioles. These contained the most complex undivided meristele of known Ferns, and the highest complexity is in those of large size. The most prominent types are shown in Fig. 283, which represents them diagrammatically in outline, but not on any uniform scale. They are all referable in origin to one "assumed primitive type" (6): this is not unlike the actual outline of the smallest of them, viz., *Dineuron* (14), or *Clepsydropsis* (7). It is elliptical in section, with protoxylems at the two foci: it has been seen in *Asterochlaena* that these originated by fission from a single protoxylem, as in the Botryopterids. From this simple type modifications appear to have arisen in two directions: first, the two ends of the xylem-strand became more or less extended, so that in simple examples the whole took a dumb-bell shape (8, 10); but in more complex forms the enlargements grew into four wide flanges, more or less curved, giving an outline as of a double anchor (9). Secondly, islands of parenchyma appeared in relation to the protoxylems (8, 9, 10). This structure has obvious relation to the pinnae, and the origin of the traces to the pinnae and to the aphlebiae is suggested in the diagrams. These early elaborations of leaf-structure in Ferns are all extinct. They have no near relation to the lines along which elaboration has proceeded in Ferns living at the present day. Hence they have little bearing upon the general morphology of modern leaves. For further details reference should be made to works on Palaeophytology.

The diagrams shown in Figs. 282 and 283 are not drawn to scale, so that they do not bring out the dilatation of the undivided leaf-trace. Those of successive leaves from the same section of *Thamnopteris* are rendered to scale in Fig. 284. The width of the largest of these, if flattened out into a plane, would be about 18 times that of the original trace. This widening must needs be related to the bifacial structure of the leaf, with its two lateral rows of pinnae. But the narrow base atavistically retained in these primitive Ferns would act as an undesirable bottle-neck. It seems, therefore, natural that in more advanced types the insertion of the trace upon the stele should be widened. This archaic disability has been removed even in such a relatively primitive type as *Loxsonia* (Fig. 275), a Fern which was carefully examined by Gwynne-Vaughan; and it will serve as a type for many Leptosporangiate Ferns of limited size. Here the meristele is a wide arc from the first, and it dilates as it passes into the petiole, attaining its greatest width near to its base of insertion on the stem. Being undivided there is little to record beyond the adoption of a rather open form, the xylem assuming in its upward course the adaxial hooks so commonly present in the leaves of Ferns. There are six protoxylem-groups, of which two occupy the abaxial angles of the curve (Fig. 285, *a*). Higher up the curve flattens (*b*), and the

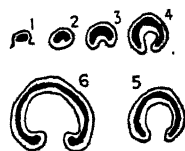


FIG. 284.

Meristele of *Thamnopteris* traced from the type specimen, showing the actual dimensions as the trace passes outwards into the leaf-base.

strands passing to the pinnae are nipped off from its margins. This marginal origin of the pinna-trace is itself a primitive feature. Higher, again, the

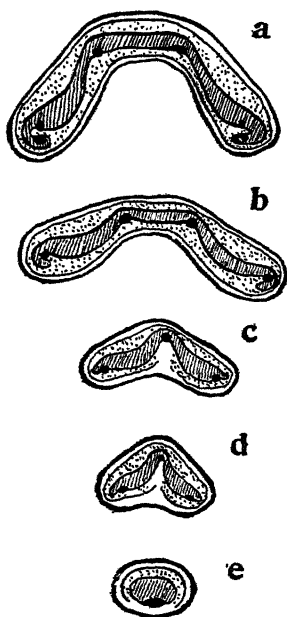


FIG. 285.

An acropetal series of sections of the meristele of *Loxsoma*, showing its modifications towards the apex of the leaf. (After Gwynne-Vaughan.)

hooks disappear, and the protoxylems are reduced to three (*c, d*), and finally to one, with collateral structure of the oval tract (*e*). This may be taken as the normal history of a foliar strand in any relatively primitive Fern. It is noteworthy how similar the last distal stage is to the original leaf-trace of *Botryopteris* or of *Thamnopteris*: this suggests that the blade of a Fern-leaf, with all its complications, is a sort of expanded interlude between base and apex, these being the regions of most primitive structure, a view which is supported by many detailed facts.

The expansion of a continuous vascular sheet, as in *Loxsoma*, enveloped in a sheath of endodermis, raises difficulties of gaseous interchange between cortex and central parenchyma. To meet this the curved meristele itself is frequently thrown into deep lateral involutions which have obvious relation to two external ventilating tracts, one on either side of the rachis (Fig. 286, 5, 6, *pp*). In most Ferns the petiole is strengthened by peripheral sclerenchyma impervious to gas-interchange. But frequently two lateral lines, continuous or interrupted, run up the leaf-stalk, and onwards to the lamina, where they are superseded

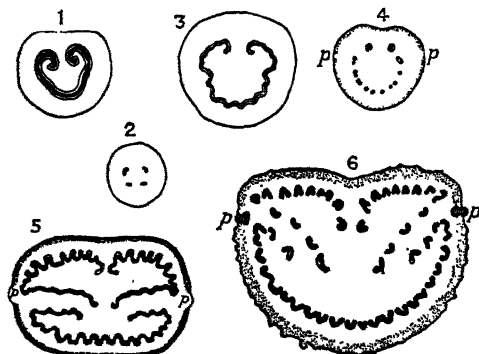


FIG. 286.

Transverse sections of petioles, all drawn to the same scale. ($\times 2$.) 1, *Dipteris conjugata*; 2, *Dipteris Lobbiana*; 3, *Metaxya*; 4, *Phlebodium aureum*; 5, *Thyrsopteris*; 6, *Alsophila*. These show that while greater size leads to vascular disintegration, there is no definite proportion. *p*, indicates the position of the pneumatophores.

by the wings of the blade. Those lines are particularly well seen in the Bracken; their surfaces bear stomata, and below them is well-ventilated parenchyma. The lines are, in fact, *pneumathodes* (Fig. 286, *pp*). Immediately below them lie deep involutions of the meristele, and together

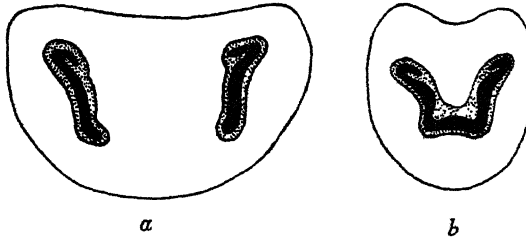


FIG. 287.

Transverse sections of the petiole of *Athyrium filix foemina*; *a*, near to the base; *b*, higher up. $\times 7$. (After Luerssen.)

they give ready access to the deeper-lying tissues of the petiole. In addition to this the vascular tract itself is frequently pierced by perforations, particularly at the base of the involutions, though present also elsewhere (Fig. 286, 5, 6). The meristele may thus appear in section to be disintegrated into units, often corresponding to the "divergents" of Bertrand and Cornaille, and ventilation is conducted through the gaps. Structurally the perforations through the meristele resemble those sometimes seen in

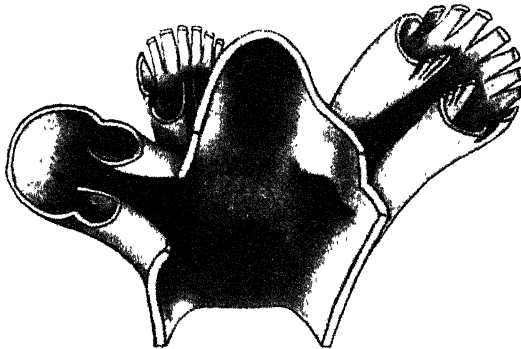


FIG. 288.

Portion of the vascular system of the stem of *Cibotium Barometz*, seen from within, and showing the departure of three leaf-traces, which become disintegrated as they pass into the petiole. (After Gwynne-Vaughan.)

the stele of the stem, and particularly in respect of the continuity of the endodermal sheaths. These gaps naturally explain what is usually described in transverse sections as the divided leaf-trace, the strands of which still follow the horse-shoe pattern (Fig. 286, 4, 6). Such disintegration of the vascular tracts is a characteristic feature of relatively advanced Ferns, as are also the cognate perforations of the stele. They are specially common at the

base of the petiole. In specific cases the leaf-trace may appear as if divided into two straps, as in *Asplenium* and *Athyrium* (Onocleoid-type of Bertrand

and Cornaille), or into many as in *Dryopteris*: these may all be separately inserted upon the lower margins of the foliar gaps (Fig. 277). The case of *Asplenium* is representative of a very general type where there is a single slit-like perforation at the leaf-base; but the gap closes as the leaf-trace is followed up the petiole (Fig. 287, a, b). Where the leaf is large the perforations of the meristele may be numerous, as in *Cibotium Barometz*. Here the leaf-trace comes away from the solenostele as a continuous sheet; but it disintegrates as it passes into the petiole (Fig. 288). If followed upwards as the rachis diminishes the meristele is reconstructed to form a single unit, with its deep lateral involutions (Fig. 289). All such states of disintegration in the leaves of Ferns are referable by comparison to the undivided meristele of the more primitive types.

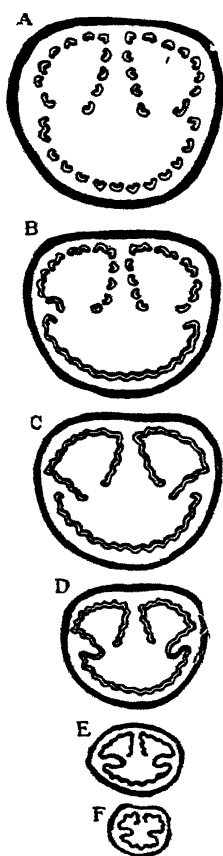


FIG. 289.

Cross sections of six different parts of a rachis of *Cibotium Barometz*, arranged in acropetal succession, showing the vascular tracts; these are highly disintegrated at the base, but re-integrated as the rachis diminishes upwards. Natural size. (After Ogura.)

VASCULAR SYSTEM. C. THE PINNA-TRACE

According to the principles of leaf-architecture for Ferns stated in Chapter XVI, the more complex leaf-forms are all referable in origin to dichotomy. The relation of the pinna-trace to the meristele of the rachis should then agree with this, though that relation may become obscure where the structure of the leaf is complicated. A simple example is seen in *Schizaea dichotoma*, where there is an equal forking of the rachis. A series of sections below the fork shows how the single meristele divides into two equal parts by a median constriction (Fig. 290, I). Various degrees of inequality of these

parts are seen on passing from one specimen to another, the smaller branch having a smaller strand. In many Ferns of primitive type, but with lateral pinnae, the pinna-trace is isolated in the same way by abstriction from the margin of the meristele. Such "marginal" origin is seen in *Pteris umbrosa* (Fig. 290, II), where the meristele with its hooked margins (i) is first extended and thinned out on the side on which the trace is to appear (ii), and

then by constriction the marginal hook with an adjoining tract of tissue is nipped off (iii). But where the meristele of the rachis is large, and particularly where it is strongly curved, the origin of the pinna-trace may be from the abaxial or convex surface of the curve. This is described as an "extra-marginal" origin, and a simple example of it is seen in *Dryopteris vivipara* (Fig. 290, III). Here the section of the rachis shows sharply incurved

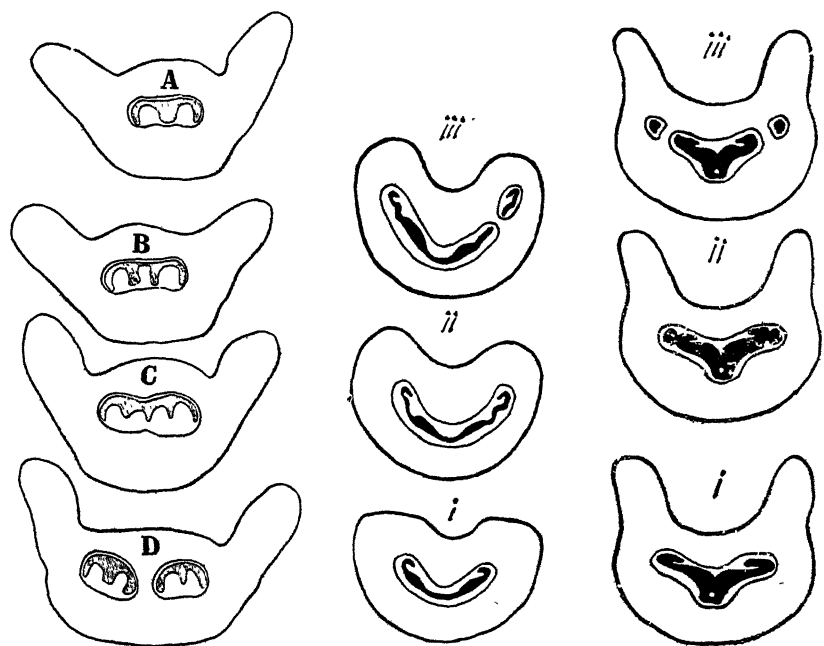


FIG. 290.

I.

A-D, Successive sections of the leaf-stalk of *Schizaea dichotoma*, showing dichotomy of the meristele; the adaxial side is uppermost. $\times 12$.

II

i-iii, Diagrams illustrating the marginal type of pinna-supply, as in *Pteris umbrosa* R. Br. (After Davie.)

III

i-iii, Diagrams illustrating the extra-marginal type of pinna-supply, as in *Dryopteris vivipara*. (After Davie.)

hooks of the xylem (i) ; at the point of greatest curvature the xylem is enlarged (ii), and the outgrowth together with its phloem and sheaths is nipped off in its upward course as the new pinna-trace, leaving the incurved hook still in position (iii). Where the meristele is widened out and laterally grooved, as in Fig. 289, the supply to the pinna is of more complex origin. The extra-marginal pinna-trace may then draw its vascular connection from both sides of the groove, a reinforcement from the abaxial curve joining with its main source of origin, which is from the adaxial curve (Fig. 291). The marginal and the extra-marginal types of origin of the pinna-trace are not essentially distinct; both may even be found in the same leaf—for instance in *Trismeria*, where the supply to the larger and lower pinnae

is extra-marginal while that to the smaller distal pinnae is marginal, the one graduating into the other. The marginal is clearly a primitive, and

the extra-marginal a derivative state: the latter appearing as a consequence of greater elaboration, and particularly where the meristele is strongly curved. The dominating biological factors appear to be, that each pinna-trace should depart from the meristele at the point nearest to the insertion of its own pinna; and that there should be as little disturbance as possible of the continuous water-supply to the succeeding pinnae, and to the distal end of the leaf. Both of these ends are secured by the extra-marginal type: the former by the departure from the point of greatest curvature of the meristele, the latter in those more complex cases where there is continuity of the hooked margins past the point of departure of each pinna-trace.

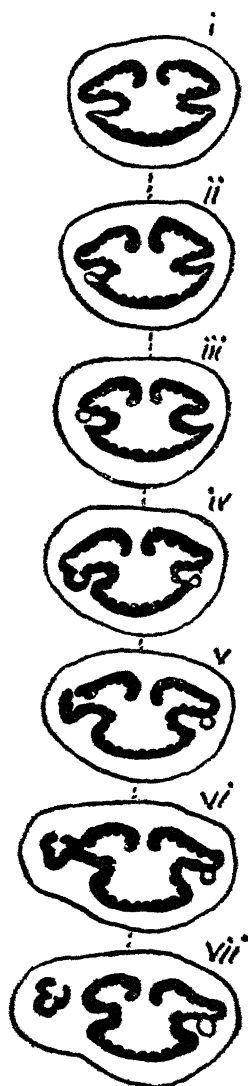


FIG. 291.

Series of transverse sections through the rachis of *Lophosoria*, successively from below upwards, showing the origin of the extra-marginal pinna-trace. $\times 4$.

VASCULAR SYSTEM. D. ROOT

There is little of interest to record as to the roots of Ferns, except among the most primitive of them. In the Leptosporangiates the stele is usually diarch, the xylem consisting of a coherent plate of tracheides, and the branching is monopodial (Fig. 291 *bis*). But in the Eusporangiate Ferns there is some latitude. For instance, in *Ophioglossum* monarch roots are found which fork distally, corresponding in these features with many Lycopods. Within the same family there may also be roots of considerable size and polyarch structure; in *Helminthostachys* they frequently have six or seven protoxylems. In the Marattiaceae roots may attain large size, with 10 or even 15 protoxylems. Wardlaw has shown that in *Danaea nodosa* while the sporeling roots are monarch the largest may have as many as 20 protoxylems (Fig. 292), and that there is a relation of their number to size comparable to that

seen in the roots of Flowering Plants (*Size and Form*, pp. 166-7). But this variability seems to have been lost in the later types: for instance, though

in *Osmunda* triarch roots are recorded they are usually diarch; and in the Leptosporangiate Ferns the latter is the rule. In the more advanced types in fact, the thin fibrous roots are highly standardised, and make up in their number for the limited size of each.

Here it will be convenient to introduce a note on the vascular anatomy of the Ophioglossaceae and Marattiaceae, together with the correlative Psaroniaceae, as a side issue: for it is difficult to assign any near derivatives to these

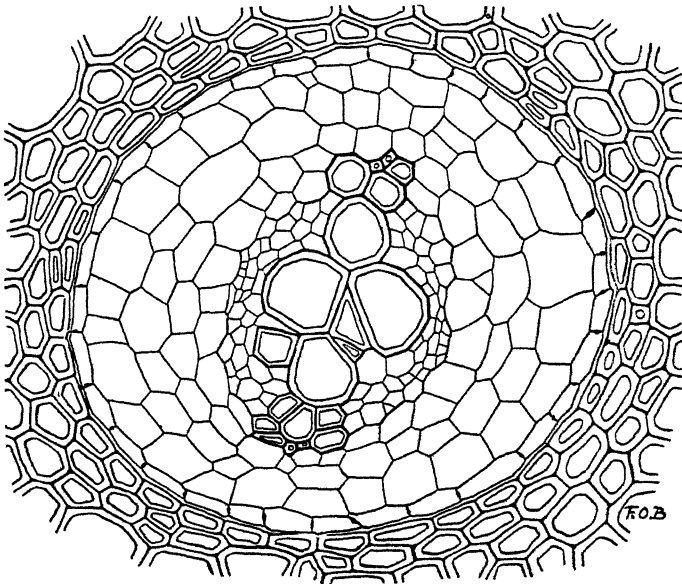


FIG. 291 bis.

Transverse section of a root of a Leptosporangiate Fern (*Pellaea*). $\times 150$. The sclerotic cortex is limited internally by a definite endodermis. There are two groups of protoxylem; a very broad pericycle, of 3 or 4 layers, surrounds the vascular tissues.

families among either living or fossil Ferns. They are all Eusporangiate, and their structure of a Palaeozoic type: nevertheless some of them possess the most highly elaborate primary vascular systems that are known. In origin these systems are essentially monostelic. For the most part they have distended, and often sappy rather than sclerotic stocks. Their leaves are commonly of leathery texture. The stems of those which have been examined in the young state possess at first a simple protostele delimited by a definite endodermis; but as this passes upwards through a medullated stage into the adult stem the endodermis often disappears, leaving the conducting tracts exposed to the surrounding tissue, a state suitable to sluggish rather than rapid transit. This contrasts with what is seen in Leptosporangiate Ferns.

In the Ophioglossaceae the stele on medullation becomes either solenoxyllic (*Helminthostachys*) or dictyoxyllic (*Ophioglossum*), but there is no advance to

typical, that is amphiphloic, solenostely. In most of them the leaf-trace comes away as an undivided strap, and the wood, except in the adult state of *Helminthostachys*, is of the primitive, purely tracheidal type. All these features indicate an archaic structure, but with tentative advances. *Ophioglossum palmatum* shows a significant step in the disintegration of the leaf-trace.

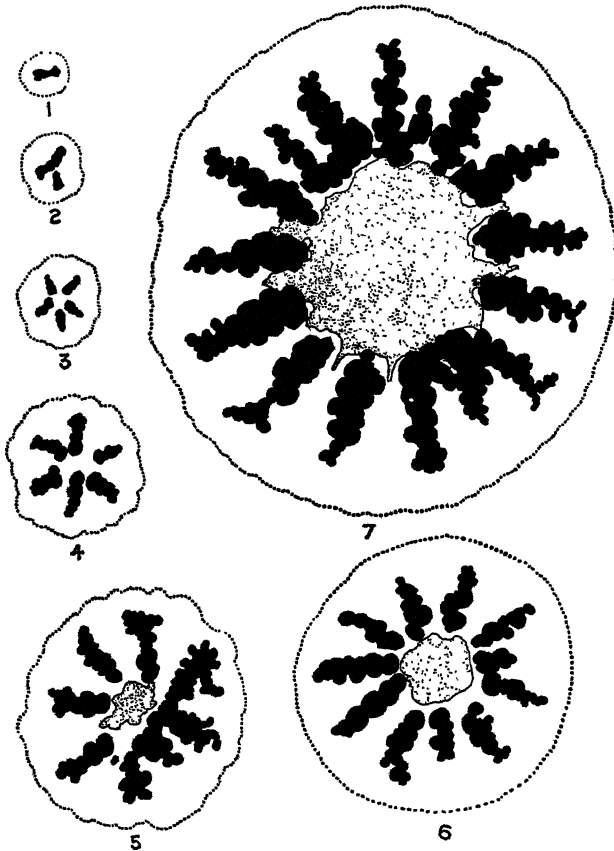


FIG. 292.

Damia nodosa. Series of sections, all drawn to the same scale, showing the changes in complexity of the xylem which accompany increase in size. 1 and 2 from sporeling plants; 3 and 4 from young plants; 5 and 6, medium sized roots from adult plants; 7, stele of a very large root. In 5-7 the pith is sclerotized. $\times 50$. (After Wardlaw.)

The stem is sappy and distended, retaining the dictyoxyletic stele, from which the leaf-traces arise as paired straps from each leaf-gap; but they break up immediately into a cycle of small strands. The roots arise from points deep-seated in the distended stock. The whole effect of this is to give the nearest approach seen among other Ferns to the Marattiaceous structure (*Ferns*, ii., p. 61, Fig. 355).

In the Marattiaceae the vascular system becomes more highly disintegrated than in the Ophioglossaceae, as the adult state is reached. This is less marked

in the smaller genera, but it comes to a climax in large plants of *Angiopteris* and *Marattia*. Nevertheless, the numerous strands may by their arrangement be referred in origin to those more continuous tracts seen in their own sporelings, or illustrated by some of the fossil types, which are less highly disintegrated. Hence the general conclusion may be drawn that these ancient stocks are only extreme examples of methods of stelar advance, based on primary structure, such as are seen in types already discussed. The stele of the sporeling expands early to a solenoxyletic state, with foliar gaps (Campbell, *Eusp. Ferns*, p. 20). This stage is soon passed over in living types, but in the fossil *Psaronius Renaulii* it appears to have been permanently retained in the adult. The state of this plant must have been similar to that of *Helminthostachys*, but of larger size, corresponding rather to that of *Cibotium Barometz*. The sporelings of the living Marattiaceae as they pass to the adult state show in varying detail the disintegration both of the central stele and of the foliar meristemes, with the result that in the stem of a large plant as many as four or five concentric cycles of isolated strands may be seen, while in a large petiole a like structure appears. This is further complicated by anastomoses, and by the origin of root-traces from deeply seated strands, these traces threading their way out through the apparent tangle. Careful dissection aided by comparison of what is seen in the fossils named *Psaronius*, in which the disintegration is less advanced, has led to the conclusion that the whole system is referable in origin to a polycyclic structure of the stem, with greatly widened foliar meristemes springing from the leaf-gaps of the outermost dictyostele. To this general conception Schoute has added a new element of precision by tracing the influence of the leaf downwards into the stem, and showing that the inner stelar systems also possess true leaf-gaps analogous to and corresponding in position with those of the outermost stele.¹ Thus the vascular system of these most complex Fern-stems is built up on a primary scheme essentially similar to that in other polycyclic Ferns. But there is still some uncertainty as to the inter-relations of the concentric steles by commissural anastomoses, and on the question whether or not strands of the leaf-trace ever penetrate in the first instance further inwards than the outermost ring of steles of the stem. In view of the fact that such connection with a medullary system is readily demonstrated in the less confused stem-structure of *Cyathea*, complete freedom from such fusions is hardly to be expected for the leaf-traces of the Marattiaceae (see De Bary, *Comp. Anat.*, Figs. 139, 141; also Godwin, "Stele of *Cyathea medullaris*," *New Phyt.*, vol. xxxi., 1932, p. 254). On the other hand, the question of the origin and relation of the many cycles of subdivided meristemes seen in the petioles of the larger Marattiaceae presents a problem parallel to but distinct from that of their stems. The similarity of the results would suggest that some common morphoplastic cause has affected them both independently. The elucidation of the meristellar system of their leaves will be best approached by tracing the system through the steps of its origin upwards, from the relatively simple leaf-trace to the full petiolar complexity, and its subsequent simplification as the extreme tip is approached. There, as Campbell has pointed out, even in the largest and most complex of these Ferns, the vascular tracts become concrete distally: in the midribs of

¹ Schoute, "Stelar Structure of Marattiaceae," *Trav. Bot. Néerl.*, xxiii., 1926.

pinnæ and pinnules "the crescent of bundles seen in the larger rachis is always completely united, and in section it appears as a single horse-shoe-shaped bundle." In fact it reverts to a comparatively simple form: while there the wood is of the primitive, purely tracheidal type, in the lower region it is "vitalised" (Campbell, *Eusp. Ferns*, p. 194, Fig. 175, *A*, and p. 194, Fig. 182, *B*; also p. 202).

As examples of the extreme polycyclic complexity of the system of the axis it may be noted that Hirmer recognises in his reconstruction for *Psaronius bibractensis* seven cycles, in *Ps. infarctus* no less than twelve (*Handbuch*, Figs. 678, 680). Edwards, in the polycyclic rachis of *Paradoxopteris* (believed to be the petiole of *Veichselia*), has found as many as eleven concentric cycles of meristeles, alternating with cycles of accessory strands; and he remarks that this structure cannot be exactly paralleled in the petiole of any living or fossil Fern (*Ann. of Bot.*, xlvii., 1933, p. 317).

CONCLUSION

The description of the vascular skeletons in Ferns given in the preceding pages may now be drawn together into a general conclusion, so far as they bear upon the evolution of the several parts. The cladode theory of the megaphyll involves a common origin of axis and leaf from an indifferent branch-system of simpler structure than either of them. But the general conformation of those parts is essentially different, a fact which determines certain structural differences. It has been seen how the axis is developed ontogenetically upon an *obconical scheme, enlarging normally upwards*, though often settling down in adult creeping Ferns to a cylindrical form; but there is no subsequent diminution—except under adverse conditions, such as starvation. The protostelic base expands upwards, in accordance with the obconical form, through successive stages of moulding and elaboration, which have been briefly described above; till finally in extreme cases the vascular system may attain a high degree of polycycly and disintegration distally. On the other hand, the cladode megaphyll also has in primitive Ferns a simple protostelic base; in the rachis this also *expands upwards*, after the manner of the axial stele though with a dorsiventral bias; but after its vascular system has attained its full size and elaborated state, the individual rachis normally *diminishes again in size*, and is simplified in vascular complexity upwards, till distally the conducting tracts may again be represented only by a simple vascular tract, structurally like that at the base. This simplified distal region of the leaf contrasts with the consistently upgrade axis; moreover, while the former is of dorsiventral the latter is usually of radial symmetry. In both, however, the vascular tracts show a like power of elaboration from a simple vascular strand at the base.

In contrast to both of these the individual root of Ferns is normally *cylindrical*: according to the size of the stele the number of protoxylem-

strands may vary from root to root, but it remains as a rule uniform in the individual organ throughout. The smallest, as seen in certain primitive types, is monarch, being traversed by a central stele with a woody core. *It thus appears that in their simplest terms the stem, leaf, and root are all alike in possessing a primitive protostelic structure*, a conclusion which receives support from ontogenetic details in the sporeling. In this respect they may all be referred anatomically to a common source, such as is presented by the most primitive of known vascular plants. Thus, putting aside the higher elaborations of each, *the skeletal structure would accord with a common origin for axis, cladode leaf, and root* (see Chapter XXVII).

The general question of the relation of the advanced vascular structure seen in the stems, leaves, and roots of Ferns to the size of the individual parts will be reserved for treatment in Chapter XXVIII, where that subject will form part of a more general discussion for Vascular Plants at large. In the present Chapter it must suffice to have traced comparatively the structural elaboration, as seen respectively in the obconical stem, the spindle-like leaf, and the cylindrical root of the Filicales : all of which have achieved that state which appears in modern examples on the basis of primary, not of cambial development.

CHAPTER XVIII

SPORE-PRODUCING MEMBERS OF THE FERNS¹

UNDER this heading are included sporophylls and sori, together with the sporangia and their protective indusia. The first leaves of any fern-sporing are usually sterile, and they are photosynthetic from the first. But the leaves of the adult commonly serve general purposes, being propagative as well as photosynthetic. This is so in the Male Shield Fern, and the two functions are usually shared over the greater part, or even the whole length of the expanded blade (Fig. 235, p. 303). But in many Ferns an opposite extreme is seen where certain leaves are broadly expanded, plagiotropic, and sterile; while other whole leaves are attenuated and fertile, standing upright as specialised sporophylls. In the Hard Fern (*Blechnum Spicant*), or the Ostrich Fern (*Matteuccia Struthiopteris*), these two types of leaves form alternating zones. In others again a definite part of the leaf may be fertile, and the rest sterile and photosynthetic; and the balance or the position of those regions may vary even within the genus. For instance, in *Osmunda regalis* the fertile state is usually restricted to the distal region, though in *O. Claytoniana* and *javanica* certain groups of pinnae, or others irregularly placed through the length of the leaf, may bear sporangia, and show a correlative reduction of their area.

The relatively primitive genus *Anemia* has always attracted attention from the fact that the two basal pinnae are in most species erect and fertile, overtopping the rest of the pinnate and sterile blade. This peculiar disposal of the fertile region, well seen in *A. Phyllitidis*, may find its biological justifica-

¹ *Selected Literature for Chapter XVIII*: Prantl, *Verh. d. Phys. Med. Ges.*, Würzburg, ix., 1875. *Die Hymenophyllaceen und Die Schizaeaceen*, Leipzig, 1875 and 1881. "Syst. d. Farne," *Arb. Kgl. Bot. Garten*, Breslau, 1892. Von Goebel, "Künstliche Vergrünung," *Ber. d. D. Bot. Ges.*, Bd. 5, 1887. Campbell, "Affinities of the Filicinae," *Bot. Gaz.*, 1890. Bower, *Journ. Roy. Hort. Soc.*, xii., 1890, p. 496. *Ann. of Bot.*, v., 1891, p. 109. Studies in Morph. Spore-producing Members; II. "Ophioglossaceae," Dulau, 1896; III. "Marattiaceae," *Phil. Trans.*, vol. 189, 1897; IV. *Lept. Ferns*, vol. 192, 1899; V. *Comparison*, vol. 196, 1903. P. Bertrand, "Stauropteris," *Études sur la Fronde des Zygopteridées*, Lille, 1909. Seward, *Fossil Plants*, vol. ii., 1910, chaps. xx.-xxvi. Chrysler, "Ophioglossaceae," *Ann. of Bot.*, 1910. *Bot. Gaz.*, li., 1911. Engler und Prantl, *Natürl. Pflanzenfam.*, i., 4, 1902; here literature to date is fully cited. Scott, *Studies in Fossil Botany*, 1920, p. 250. Bower, "Studies in Phylogeny of Filicales," i.-vii., *Ann. of Bot.*, 1910-1918. Hirmer, *Handbuch*, 1927, p. 484, etc., with full citation of fossils. Von Goebel, *Organographie*, 1930, Teil ii., pp. 1258-1324. Bower, *The Ferns*, vol. i., chap. xii.; vols. ii., iii., *passim*.

tion in easy access of nutriment, and convenience for spore-distribution. The small rock-growing Brazilian species, *A. (Trochopteris) elegans*, is interesting for comparison with this more familiar type; the construction of its flattened leaf is shown in Fig. 293. The dichopodial venation and lobing are of the same plan as in the sporelings of *Osmunda* (Fig. 238). The two lowest pinnae bear isolated or grouped sporangia on the vein-endings of the spatulate lobes. But other sporangia are frequently found on the upper lobes also, and even at the distal end of the leaf: this gives a state comparable with what is normal in the allied genus *Mohria*. Thus the whole leaf appears to be potentially fertile, though normally the fertility in *Anemia* is localised in the lower pinnae only. The homology of the sterile and fertile parts in the leaves of Ferns has been demonstrated experimentally by Von Goebel. By removing early in the season those leaves of the Ostrich Fern (*Matteuccia Struthiopteris*) which would normally be photosynthetic and sterile, he succeeded in inducing those which succeeded them, and would normally be fertile, to develop as photosynthetic leaves: moreover, various intermediate states were produced between the two. Such results, taken together with general comparison of sterile

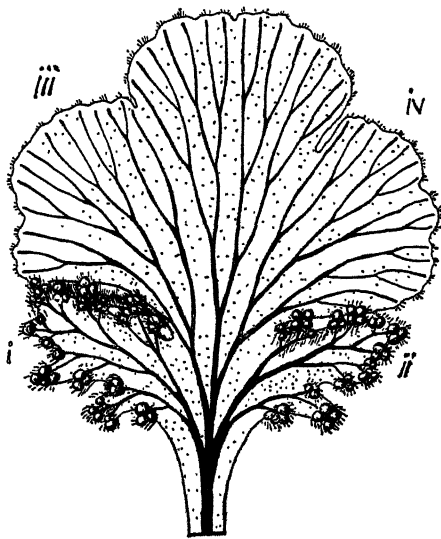


FIG. 293.

Fertile leaf of *Anemia (Trochopteris) elegans*, showing symphyllal dichotomous branching of its veins; i-iv = successive pinnae; the two basal pinnae are fertile, but sporangia are sometimes found also on the upper segments or at the distal end, as in other species of *Anemia* (see Von Goebel, *Flora*, 1915). $\times 4$.

and fertile leaves for Ferns at large, suggest as a probable working hypothesis that the cladode leaf is throughout potentially fertile; but that the juvenile leaves, and parts or even the whole of the adult leaves, may be developed sterile, though the remainder may be fertile. Nutrition already achieved may well be a determining factor in promoting fertility, and in particular some increase in the available ratio of carbohydrates to mineral substances (Von Goebel, *l.c.*, pp. 1234-8). The conclusion thus drawn from comparison and experiment within the Filicales will be of special value in the broader morphological treatment not only of Ferns themselves but also of the Pteridophytes at large (see Chapters XXIX-XXXI).

The type commonly used for elementary illustration of the sorus is the Male Shield Fern, which has been described with sufficient detail in *Botany of*

the Living Plant, Chapter XXXI, or in the *Land Flora*, Chapter II. This Fern may be held as a medium rather than an extreme type : it has been chosen for students as an average representative of the Leptosporangiate Ferns. The clearly defined features of its sorus suggest that it consists of a standardised group of organs including numerous sporangia, a circumscribed receptacle on which these are seated, and the whole covered by an indusium of characteristic form (Fig. 235). But comparison of Ferns at large

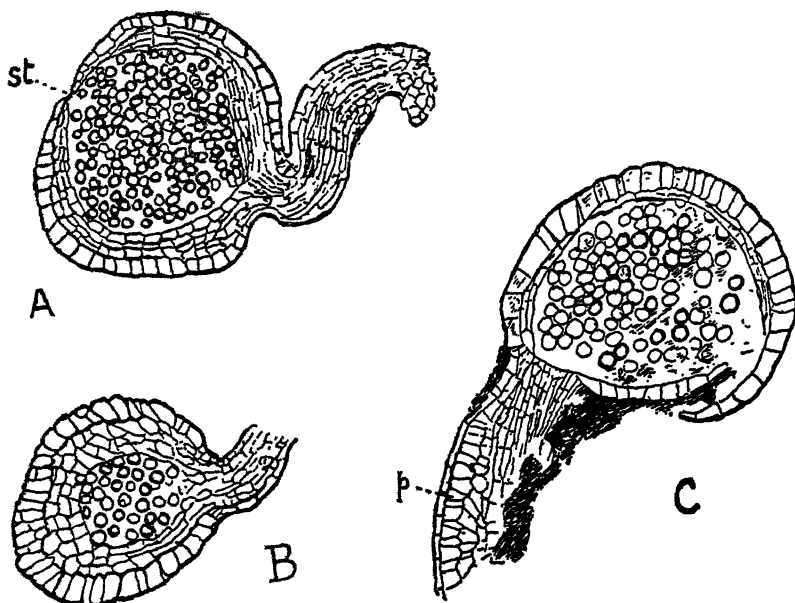


FIG. 294.

Stauropteris Oldhamia, Binney. A=sporangium in nearly median section, attached terminally to an ultimate branchlet of the rachis: st=stomium. Scott Coll., 2213. B=sporangium in tangential section attached to a short piece of branchlet. Scott Coll., 2207. C=sporangium with wall burst, attached as before. p=palisade tissue of branchlet. Scott Coll., 2219. All figures \times about 50. (From sketches by Mrs. D. H. Scott. The specimens are from Shore, Littleborough, Lancs.)

shows that there is very wide latitude in the form, composition and distribution of those groups of organs to which the term sorus has been applied ; and that the differences yield data which, when checked by comparison with related fossils, give a field of evidence upon which a consecutive evolutionary story may reasonably be founded. In treating the Class comparatively as regards its spore-producing members the same sequence of illustration will be adopted as with the external morphology (Chapter XVI), and their anatomy (Chapter XVII) : viz., to take first the Eusporangiate types and to proceed from these along lines believed to be those of phyletic advance to the Leptosporangiate Ferns (see p. 324, Fig. 259). The effect of this should be to build up comparatively some reasonable conception of how a complex sorus such as that of the Male Shield Fern may have come into being.

The simplest state of all in any plant recognised as a Fern may be seen in *Stauropteris*, a fossil usually referred to the Coenopteridaceae, and dating back to the Lower Carboniferous period. Here each sporangium stands isolated on the end of an ultimate branchlet of the forking frond, which shows the usual anatomical characters, including a thin vascular strand traversing the stalk (Fig. 294). The capsule is approximately spherical, about 0.7 mm. in diameter, with a wall composed of several layers of cells, the outermost enlarged and strengthened. There is no specialised annulus, but a well-marked stomium appears at the distal end. The size varies, but the spore-output of a large one may be estimated at about 1000. The spores are all alike, and are sometimes seen to have germinated within the capsule, as they do in certain living Ferns. The sporangia are of the Eusporangiate type, though more rudimentary than in living Ferns; and if the word sorus be applied, each would be in Prantl's terminology "Monangial."

The term sorus is derived from the Greek *σῶρος* = a heap. In its original sense therefore it does not include any protective indusium, while it implies a plurality of the constituent sporangia. Hence the introduction by Prantl of the conception of a "monangial sorus" is a contradiction in terms. His use of it was originally in describing various forms "in which the sorus is reduced to a single sporangium" (*Verh. d. Phys. Med. Ges.*, Würzburg, Bd. ix., 1875, p. 84). But as applied to *Lygodium* he includes the indusial flap ("Ein Sporangium nebst Tasche," *Die Schizaeaceen*, Leipzig, 1881, p. 43). By this recognition in 1875 of a sorus with a single sporangium Prantl laid the foundation for the modern morphology of the Fern-sorus. He pointed out as examples of it the Ophioglossaceae and Schizaeaceae, particularly the genera *Lygodium* and *Anemia*. His comparisons were, however, based on a theory of reduction from sori where the sporangia are numerous. Moreover, he conceived the origin of the simpler Leptosporangiate Ferns, and particularly the Hymenophyllaceae, to have been from the Bryophytes, and that the Eusporangiate Ferns were again derivative from them, thus conforming to the views prevalent at the time. It was not till 1890 that Campbell claimed priority for the Eusporangiate Ferns (*Bot. Gaz.*, 1890), a view at once accepted by others (Bower, *Journ. Roy. Hort. Soc.*, N.S., xii., 1890; *Ann. of Bot.*, v., 1891, p. 109). This opened the way for comparisons such as more recently discovered fossils suggest. The whole of Prantl's thesis thus needs to be inverted. But this in no way detracts from the merit of his recognition of the "monangial sorus" as a feature of observation highly important in the morphology of the sorus at large; and it is actually seen in its simplest form in *Stauropteris*.

In the Zygopterid fossil *Etapteris* the sporangia were borne not singly but in groups upon a common stalk, through which a vascular strand passed, dividing into smaller strands which traversed the several pedicels (Fig. 295, 1, 2).¹ The sporangial wall consisted of at least two layers, the outer having

¹ In the terminology to be adopted later the stalked sporangium of *Stauropteris* would be a single "Telome"; the group of sporangia of *Etapteris* a "Telome-Truss," chap. xxix.

larger cells, and differentiated so that several rows formed an indurated band running up each side vertically to the summit, and forming a mechanical loop as in *Angiopteris*. A group or tassel of these sporangia cut transversely shows that they were orientated round a centre, as they are in the radial sori of the Marattiaceae and Gleicheniaceae (3). In fact each group is a lax

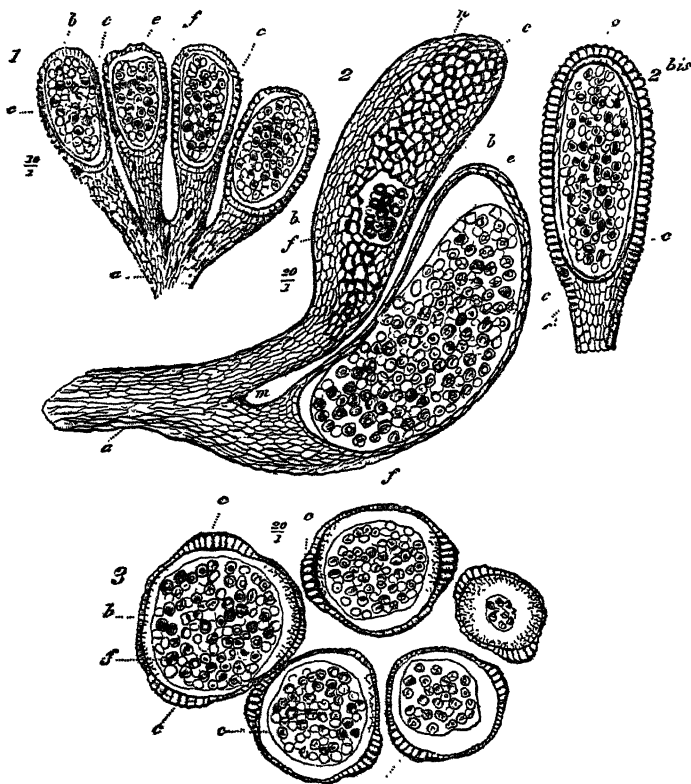


FIG. 295.

Eptaeteris Lacatieri. 1, group of four sporangia on a common pedicel (a). $\times 10$. 2, two sporangia on pedicel. The upper shows the annulus (c) in surface view, with spores exposed at f; the lower in section. $\times 20$. 2 bis, sporangium cut in plane of annulus. 3, group of sporangia in transverse section. $\times 20$. Lettering common to the figures. a, common peduncle; b, sporangial wall; c, annulus; e, tapetum (?); f, spores; m, pedicel of individual sporangium; n, probable place of dehiscence. All after Renault. (From Scott's *Studies in Fossil Botany*.)

uniseriate sorus, though each sporangium has its own vascular pedicel. Here again the spore-output of each sporangium is estimated at about 1000. If the stalks, as seen in *Eptaeteris*, were shortened, and the sporangia still more closely grouped but with the same orientation, the condition seen in *Corynep-teris* would result (Fig. 296). Here each group is seated on a common receptacle, and is in fact a radial sorus essentially of the Marattiaceous type. The existence of a separate annulus to each sporangium makes it probable

that in *Corynepteris* the sporangia were not actually coalescent as in *Marattia*, but separate as in *Angiopteris*. These three fossils, viz., *Stauropteris*, *Etapteris*, and *Corynepteris*, suggest an origin for the uniseriate sorus. From their comparison it seems legitimate to regard that type of sorus as a condensed tassel of branchlets, each bearing a solitary distal sporangium; alternatively each branchlet of these might itself be styled a "monangial sorus" of Prantl.

Very similar conditions are seen in *Botryopteris*, where the sporangia differ in having the multiseriate annulus only on one side; but the spore-output is about the same. Scott has shown in *B. antiqua* that here also the sporangia are grouped round a centre, with the thinner dehiscient region of

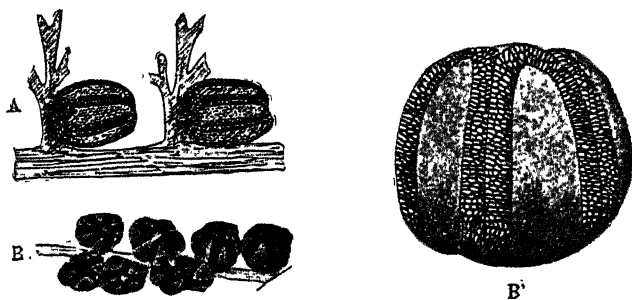


FIG. 296.

A = *Corynepteris Essenghi*, Andræ (sp), from the Westphalian. Fragment of a fertile pinna. $\times 6$. B = *Coryn. coralloides*, Gutbier (sp), from the Westphalian. Fragment of a fertile pinna. $\times 4$. B' = sorus of the same species seen laterally. $\times 28$. (After Zeiller.)

the wall directed outwards, while between the sporangia lies an "indusium-like" structure comparable perhaps with the lacinate growths found distally on the sporangiophores of *Helminthostachys* (see Fig. 299, g). From these brief notes it appears that the Coenopterid Ferns of the Carboniferous Period present states suggestive for comparison on the one hand with the Rhyniaceae type of Devonian plants, and on the other with types of sori and sporangia still retained by Ferns now living. In fact such a series as that quoted above may be held as synthetic between the "monangial sorus" of Prantl actually present in *Stauropteris* or *Hornea*, and the uniseriate sorus of the Marattiaceae or Gleicheniaceae.

In their bearing on such comparisons the living Ophioglossaceae present many interesting features. The general habit of these plants, with their underground stock and large usually solitary leaves, is seen in Fig. 297. The most characteristic feature is that each leaf may consist of a "sterile lobe," simple or branched, bearing a "fertile lobe" or spike attached on its ventral face: this also may be simple or branched, but it bears numerous sporangia with a correlative limitation of surface. Often the fertile lobe is apparently absent; but examination shows it, minute and abortive, even in

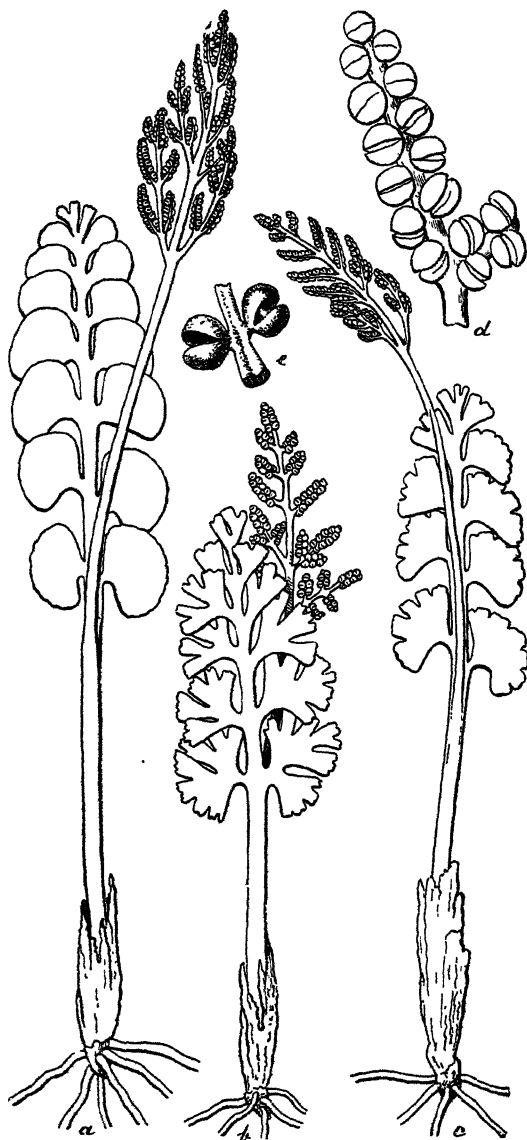


FIG. 297.

Botrychium Lunaria, Sw. *a*=*forma normalis*, Roep. ; *b*=var. *incisa*, Milde ; *c*=var. *subincisa*, Roep. All of natural size. *d*=part of the fertile spike, with open sporangia, enlarged ; *e*=two open sporangia somewhat bent asunder, to show their attachment, enlarged. (From Luerssen in Rabenhorst's *Krypt. Flora*.)

relatively young sporelings. Efforts have been made to give an interpretation of this unusual feature in terms of ordinary Fern-leaves ; and the origin of the vascular supply has been held as supporting a pinna-origin of the fertile spike (see Chrysler, *Ann. of Bot.*, 1910, p. 1 ; *Bot. Gaz.*, lii., 1911, p. 151 ; Bower, *Ferns*, ii., p. 64). The conclusions from this source, as also from the early development, have never proved fully convincing, even for *Botrychium* ; while the varieties in position and branching of the fertile spike seen in other representatives of the Family do not follow the lines usual in the morphology of the more advanced Ferns. In view of the relatively primitive features of the sporangia themselves it would seem preferable to seek an elucidation of the peculiar morphology of the Ophioglossaceae not among these, but rather among those early vascular plants in which the morphological differentiation is less determinate. Certain developmental and anatomical data would harmonise with an antero-posterior dichotomy, of which one limb becomes photosynthetic and the other fertile : the latter being delayed in its development in accordance with its function (*Ferns*, ii., Fig. 360). Bruchmann's latest observations on *Botrychium* show that the spike originates nearer to the apex of the sterile blade than in *Ophioglossum*, and probably from the latest adaxial segments of the leaf-initial. Such facts support a theory of dichopodial origin, while the fact that the sterile blade may not uncommonly be itself fertile points in the same direction (*Ferns*, ii., Fig. 338). The individual sporangia of *Botrychium* are borne separately in acropetal order on the margins of the segments of the fertile lobe ; their alternate insertion suggests a further dichopodial origin. Each has a short thick stalk traversed by its own vascular strand, which terminates below the capsule. The sporangia are massive, with a wall composed of several layers of cells, and the spore-output is large (1000 to 2000). The sporogenous tissue of each normal capsule originates from one parent cell, which is the inner product of a single superficial cell (Fig. 298, *A-C*). But the identity of the sporangium thus constituted is not always maintained ; two or more may be formed apparently coherent together. Developmentally this is the result of a partial or complete fission of the sporogenous tissue, and various intermediate states may easily be found in *B. Lunaria* or *daucifolium* (Fig. 298, *D-G*). This suggests incomplete dichotomy of the sporangium, of a type seen in *Hornea* (Kidston and Lang, ii., pl. ix., Fig. 58). At ripeness the dehiscence is by a distal slit (Fig. 297, *d, e*) (compare also Fig. 441, Chapter XXIX).

The other allied genera differ in the relations of their sporangia. The coherent spike of *Ophioglossum* may well have resulted originally from a fusion combined with fission of sporangia of the type of *Botrychium* : they form a continuous row on either side of the fertile spike (Fig. 299, *A, B*). The spike itself may, however, be branched, and even a plurality of spikes be produced, corresponding more or less regularly with lobes of the usually

entire sterile blade, as in *O. palmatum* (*Land Flora*, Figs. 238, 239). It has been suggested that this increase is by pleiomery, comparable with that of the sporangiophores of *Sphenophyllum*, or of the stamens of many Angiosperms (*Ferns*, ii., p. 90). If this be a true interpretation, and *Ophioglossum* be a derivative type, this would accord with the advanced reticulate venation of its leaf, as against the primitive open venation of the other genera.

On the other hand, *Helminthostachys* presents a diffuse structure of the spike. It is inserted as before on the ventral face of the sterile blade, which

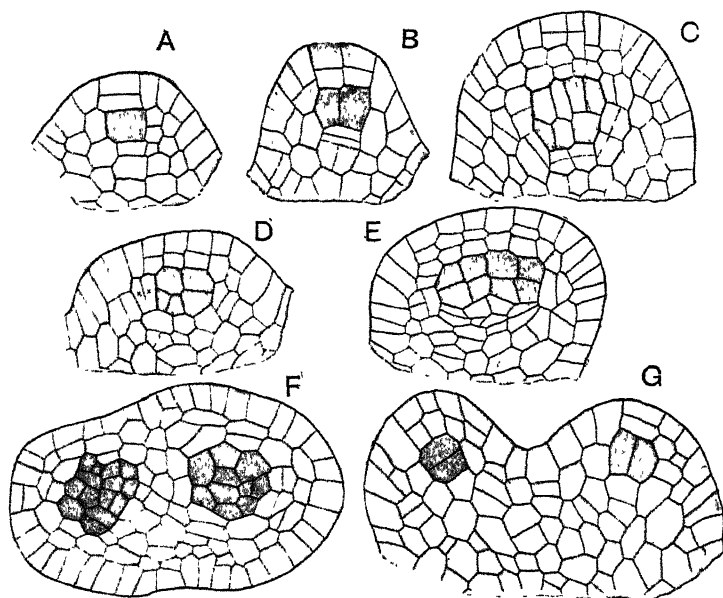


FIG. 298.

Botrychium daucifolium, Wall. A and C, successive stages of the most common type of sporangium. B—a small sporangium of narrow form. D—a very broad sporangium; the cells marked (x) correspond to the sporogenous group, but showed no signs of developing further as such. E—a still broader sporangium with wide sporogenous group, referable to two parent cells, perhaps ultimately to one. F, G=synangia cut transversely and vertically. $\times 200$.

is here branched with a pedate tendency (Fig. 299, F). Borne right and left on it are serried ranks of sporangiophores covering the margins where in other genera the sporangia are seated (Fig. 299, G). They vary greatly in size and in number, and in the tale of sporangia which each bears; while a vascular supply enters each sporangiophore from the spike itself (Fig. 300, a, b, c). The irregularity in size and position of the sporangiophores is exceptional among spore-producing parts, which are usually more standardised. They arise in rounded form, and the sporangia are developed as outgrowths from them, with structure as in *Botrychium* (e, f). As these approach maturity the distal end of each sporangiophore may produce a rosette of vegetative laciniae, comparable perhaps with the growths already noted in *Botryop-*

teris (Fig. 299, *G*). The whole structure is unique among living plants. The spike is certainly the correlative of those of *Botrychium* and *Ophioglossum*; but it seems doubtful whether it represents a state of elaboration from these, or rather of condensation from some highly branched Zygoterid source. In either case the attempt to resolve their structure in terms of more highly

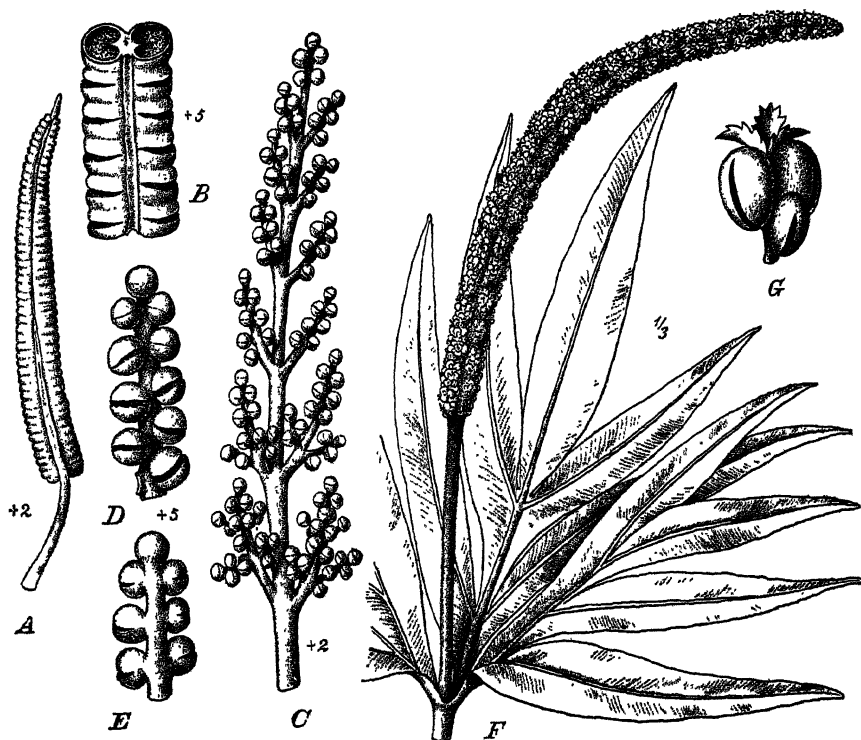


FIG. 299.

A, B, Ophioglossum palmatum, L. *A*=a single fertile spike with sporangia still closed. *B*=part of the same with sporangia ruptured. *C-E=Botrychium Lunaria*, Sw. *C*=a fertile spike. *D*=a branch of the same with ruptured sporangia, seen from within. *E*=the same seen from without. *F, G=Helminthostachys zeylanica*, Hook. *F*=sterile and fertile regions of the leaf. *G*=branch of the latter with a group of sporangia, and at the apex the lamina-like terminals of the fertile appendage. (After Bitter in Engler and Prantl, *Nat. Pflanzensfam.* *D* after Luerssen. *F, G* after Hooker-Baker.)

specialised leaves of Ferns will not succeed. The spikes of the Ophioglossaceae are best ranked among parts of indeterminate character, such as many of the earlier vascular fossils present. Taken together the Ophioglossaceae do not appear to have advanced to a true soral state, as that is understood in other Ferns. Their spore-producing members are all based upon the "mon-angial sorus" of Prantl, combined with varied development of the spike upon which the individual sporangia are borne (see Chapter XIX for further details).

The ancient Coenopterid Ferns have already given clues leading towards the radiate-uniseriate sorus as it appears in the Marattiaceae. That type was represented in the Carboniferous period by *Ptychocarpus unitus* (Fig. 301), where the sorus was superficial, as it may possibly have been also in *Corynepteris*. This is clearly its position in the modern Marattiaceae, where each is seated on the lower surface of the flattened blade (Fig. 302). In *Angiopteris*

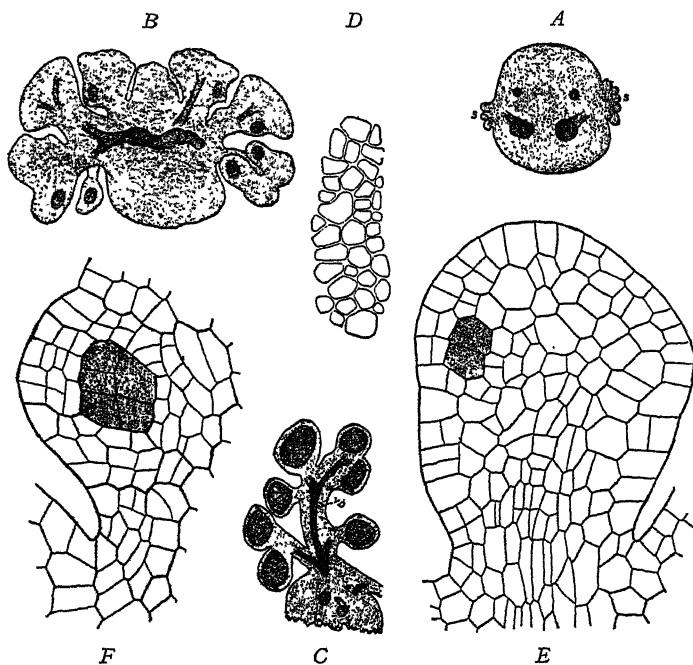


FIG. 300.

Helminthostachys: A, transverse section of a young spike, near to the base of the fertile region, enlarged, showing sporangiophores (s); B, section of an older spike, near to the tip, with sporangiophores ($\times 12$); C, a single large branched sporangiophore, with sporangia; D, young sporangiophores seen from above, showing the variation of size ($\times 24$); E, sporangiophore with one young sporangium ($\times 200$); F, an older sporangium ($\times 200$).

(A) and *Marattia* (C) the sori lie close to the margin, but in *Danaea* (E) and *Archangiopteris* (B) they extend along the veins towards the midrib, while in *Christensenia* (D) they are dotted over the broad surface. The sori are sessile, or shortly stalked as in *M. Kaulfussii*, each consisting of numerous massive sporangia disposed in a single regular series round a central point (*Ptychocarpus*, *Christensenia*), or a more or less elongated line (*Angiopteris*, *Marattia*, *Archangiopteris*, *Danaea*). Its form is therefore variable though its constitution is uniform (Fig. 302). There is evidence, however, that the identity of the sorus is not always maintained: in partially fertile pinnae, and frequently in the normal blade of *Christensenia*, states of fission are found: this

probably explains the origin of their spread in the latter Fern (Figs. 302, *D*, and 320). A vascular supply extends into the receptacle in *Ptychocarpus* (Fig. 301), and in *Christensenia* also; but it does not take the form of a definite strand to each sporangium. These developments may all be traced as springing from an originally tassel-like source. In *Angiopteris* and *Archangiopteris* the sporangia are still distinct from one another, and there is a separate opening mechanism for each, as in *Corynepteris* and *Etapteris*, and less efficiently in *Botryopteris*. But where there is fusion of the sporangia, as in *Marattia* and *Danaea*, the individual mechanism is absent. The same type, but on a smaller scale both in number of sporangia and in their size, is seen in the superficial sori of *Gleichenia*, where again the sporangia are all separate. This genus will be dealt with later as a starting point for the more advanced "Superficiales." By the comparisons here indicated it appears that all the types of sorus so far mentioned are referable to an origin from separately stalked sporangia, and in the first instance they probably formed part of a profusely branched frond with distal sporangia, as in *Stauropteris*, or were seated on or near to the margin of narrow cladode branches, such as were characteristic of a vegetation that preceded the stabilised formation of a broad leaf-blade.

It has already been seen that the Osmundaceae, which date back to Permian time, take a middle position between the Eusporangiate and the Leptosporangiate types, as regards their vegetative form and structure. In the grouping of their sporangia it is the same: the rather large capsules are borne in *Osmunda* in approximately marginal tassels on the narrow fertile segments, but without any regularity of their grouping, or of the orientation

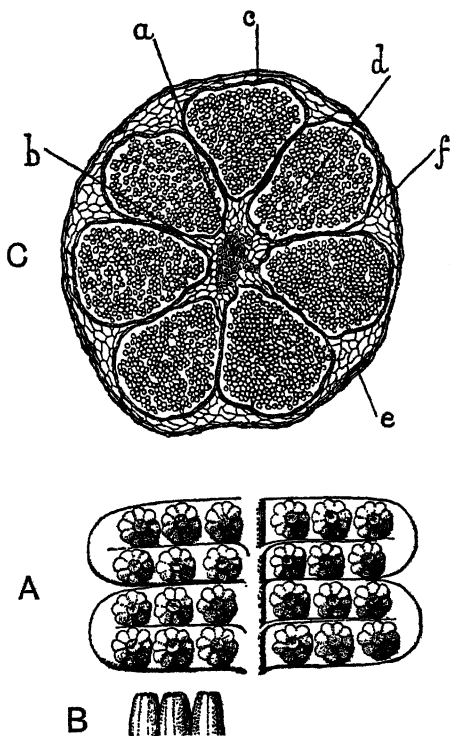


FIG. 301.

Ptychocarpus unitus. Fructification. *A*, part of a fertile pinnule (lower surface), showing numerous synangia. *B*, synangia in side view. (*A* and *B* \times about 6.) (After Grand' Eury.) *C*, a synangium in section parallel to the surface of the leaf, showing seven confluent sporangia. *a*, bundle of receptacle; *b*, its parenchyma; *c*, tapetum; *d*, spores; *e*, *f*, common envelope of synangium. \times about 60. (After Renault.) From Scott's *Studies in Fossil Botany*.

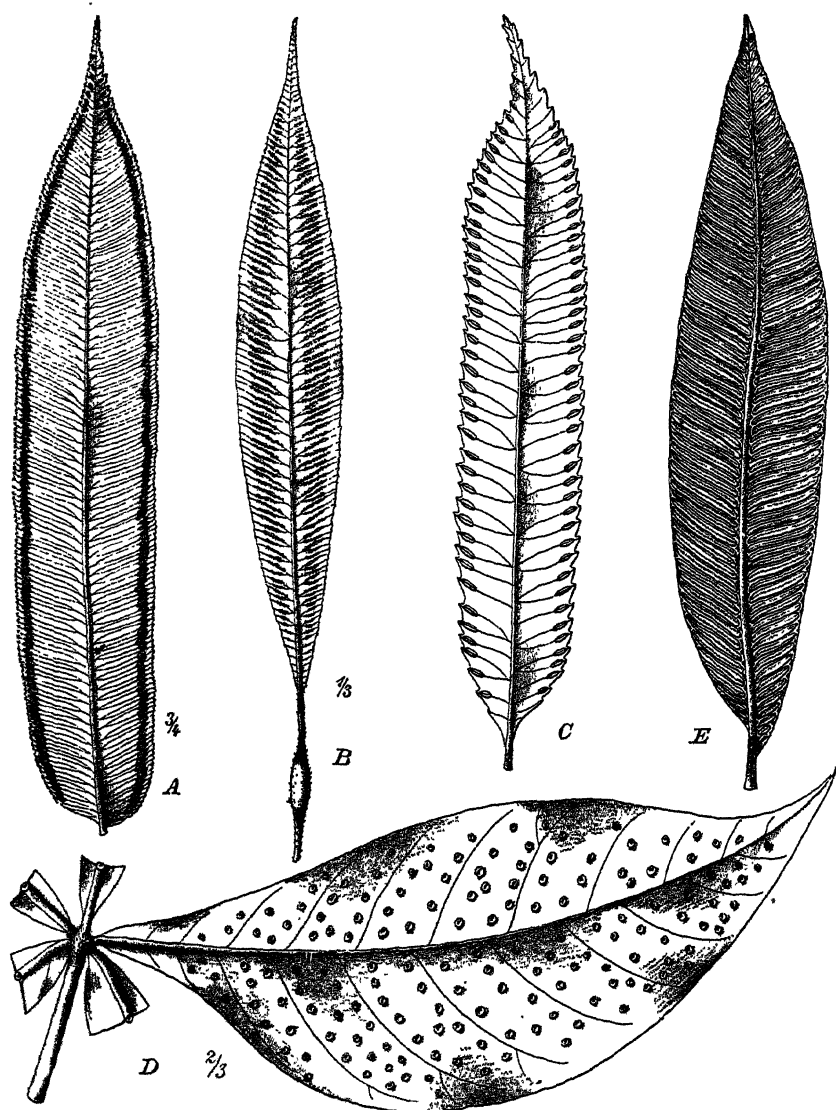


FIG. 302.

Pinnae of the five genera of the Marattiaceae, all of them lateral pinnae. *A* = *Angiopteris crassipes*, Wall.; *B* = *Archangiopteris Henryi*, Christ and Gieslen.; *C* = *Marattia fraxinea*, Sm.; *D* = *Christensenia asculifolia* (Bl.) Maxon; *E* = *Danaea elliptica*, Sm. *A*, *C*, *D*, *E* after Bitter; *B* after Christ and Giesenhagen. (From Engler and Prantl, *Nat. Pflanzenfam.*)

of the sporangia. Their lax arrangement allows the elbow-room necessary for effective dehiscence (Fig. 303, III.). But in *Todea* the sporangia are borne on the lower surfaces of the broader leaf-segments, and they lie spread out along the veins, though not grouped into definite sori, and with no rule of orientation. In *Osmunda* intermediate states between the sterile and fertile leaf-segments have been found, with extended blade and sporangia borne superficially on its lower surface (Fig. 303, I., II.). The probable conclusion is that the marginal position was the original one, but that with widening of the leaf-expanse the sporangia are liable to be shifted to the lower surface, as the sori are in the Marattiaceae. In fact, that *Osmunda* normally shows in this respect a primitive, and *Todea* a derivative state.

In the Schizaeaceae, which date back certainly to Jurassic and probably to Carboniferous time, the sporangia are again non-soral. As Prantl first showed in detail, their origin is solitary and strictly marginal. This has been demonstrated for all the genera, notwithstanding that the insertion soon becomes superficial in appearance, owing to early and strong growth of tissue on the adaxial side, which forces each sporangium towards the lower surface (Fig. 304). This growth introduces a new feature, viz., a protective flap, which takes various forms within the family. The details of it suggest steps in the origin of an indusium.

All the Ferns whose spore-producing members have so far been described have sporangia of relatively large size. They are all fully Eusporangiate, excepting the Osmundaceae and Schizaeaceae, which occupy an intermediate place. They all form their sporangia simultaneously so far as the individual leaf-segment or sorus is concerned. Since there is no succession of appearance of the sporangia the drain of nutrition for them all falls at the same time on the part that bears them. Moreover, there is in them free exposure of the sporangia while yet young; there is little or no protection in the Ophioglossaceae, Marattiaceae, or Osmundaceae, beyond that which their own crowded stance or the leaves as a whole afford. Even the marginal position, which naturally risks exposure of the sporangia, is often retained, though in the Marattiaceae and Schizaeaceae and in *Todea* the passage of the sporangia towards the lower surface affords relief. These families show

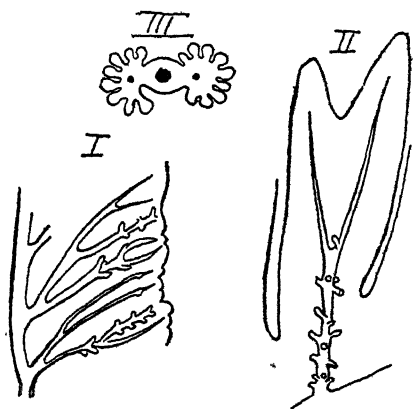


FIG. 303.

I, *Osmunda regalis*, part of a metamorphosed sporophyll, with stalks of aborted sporangia attached superficially; II, *Todea pallucida*, part of a pinnule with sporangial stalks. III, Transverse section of a fertile pinnule of *Osmunda*, showing normal insertion of the sporangia. (All after Von Goebel.)

a primitive and biologically undesirable state which was prevalent in those of early palaeontological time. The Ferns having these characters have been styled the *Simplices*, and though some of them still survive they are plants characteristic of the Palaeozoic period rather than of the present day. It is from such sources that the modern types of Ferns must needs have sprung.

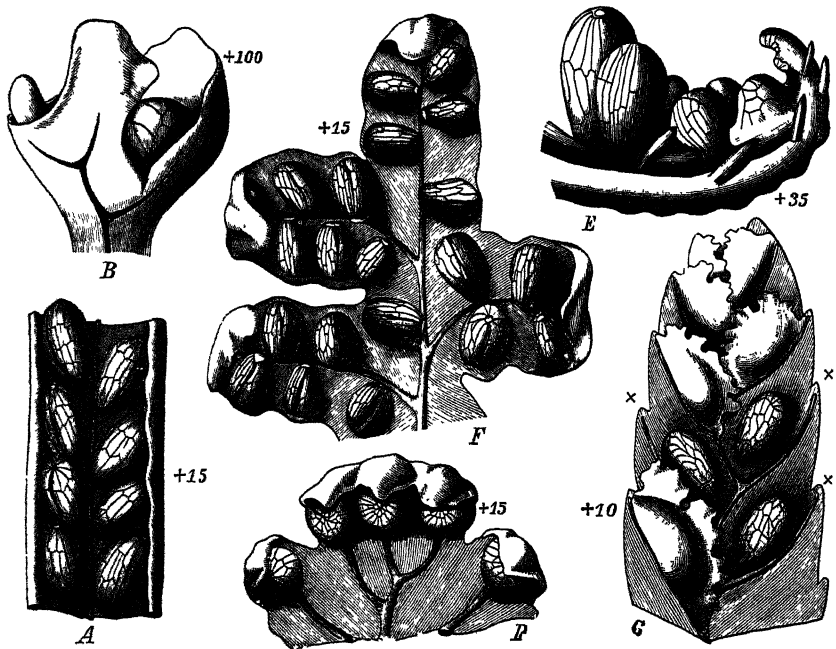


FIG. 304.

Disposition of the sporangia of the Schizaeaceae. *A*=*Sch. dichotoma*, J. Sm., part of a fertile segment (sorophore). *B*, *C*=*Lygodium japonicum*, Sw. *B*=apex of a young fertile segment. *C*=mature fertile segment; at (x) the sheaths have been removed, so as to display the sporangia. *D*=*Mohria caffrorum* (L.) Desv., segment of a fertile pinna. *E*, *F*=*Anemia phyllitidis*, Sw. *E*=side view of a young fertile segment. *F*=fertile segment from below. (*A*, *B*, *E* after Prantl. *C*, *D*, *F* after Diels: from Engler and Prantl, *Nat. Pflanzenfam.*)

We may not be able to trace the lines of descent with certainty, but the primitive types already possess many of the leading features which have been worked out in greater detail in the Leptosporangiate Ferns.

With this general view, supported as it is by palaeontological evidence, we may proceed to a comparative sketch of the spore-producing members of modern Ferns. The treatment should be organographic rather than severely morphological. In the first place the biological requirements may be considered, and later the means by which those requirements have been met in the course of evolutionary change. Since those demands will fall independently upon any progressive stock or phylum, polyphyleticism may be anticipated; and its recognition naturally follows from a comparative study

of the more advanced Ferns, if carried out along these lines. The biological ends to be served by adaptation of the spore-producing parts of Ferns are : (1) a prolific production of spores ; (2) their effective nutrition ; (3) their protection during development ; and (4) their mechanical distribution. These ends have been attained with great variety of detail, by multiplication of sporangia ; by their concentration on receptacles with common vascular supply, and often by soral fusion, thus giving more effective access to the general conducting system ; by successive instead of simultaneous development, whereby the drain of nutrition is spread over a prolonged period ; by transfer of the sori or sporangia to the abaxial surface of the leaf, and by the production of various indusial growths, which cover them more effectively than the mere mutual protection by close crowding ; finally, by elaboration of the ejaculatory mechanism. The variety of detail by which these ends have been attained, severally or collectively, is very great ; and it has provided the chief data for the systematic treatment of this large Class. But such progressions in the propagative region do not necessarily run parallel with other morphological characters, such as external form, or vascular anatomy. This complicates the recognition of natural affinities, and has led to frequent misunderstanding ; and as a consequence to a profuse synonymy. This whole subject has been dealt with at length in *Ferns*, vols. i.-iii., Cambridge Press. Here the advance in soral characters will be traced only along its main lines. The most important of those soral changes which may be recognised in the evolutionary progression will be described under the following headings :

- (1) Change in position of the sorus.
- (2) Succession in appearance of the sporangia.
- (3) Protection of the sorus.
- (4) Soral fission, fusion, and disintegration.

CHANGE OF POSITION OF THE SORUS

In the Coenopterid Ferns a marginal position of the sporangia is prevalent, a feature significant for comparison with their distal position as seen in early types of vegetation. This is their constant point of origin in the living Schizaeaceae, a family in which the sporangia are habitually isolated, as they are seen to be in *Schizaea*. Here they arise directly from the marginal row of cells (Fig. 305, *B*). But as they develop the marginal origin may be disguised by subsequent displacement ; for instance, to form two rows as in (*A*), and by shifting towards the lower surface : this is combined with various indusial developments, as already noted (Fig. 304). Such observations form a starting point for a considerable series of Ferns which have been styled *Marginales*, and include the Hymenophyllaceae, Dicksoniaceae, and Pteroidae. They are characterised by varying degrees of departure of the

sporangia from that marginal position which is seen so conspicuously in the Schizaeaceae, and thus they illustrate gradual steps towards insertion of the sorus on the lower leaf-surface.

The marginal stance of the sorus is strictly maintained in the Hymenophyllaceae, though in the Loxsomaceae the adult sorus faces obliquely downwards.

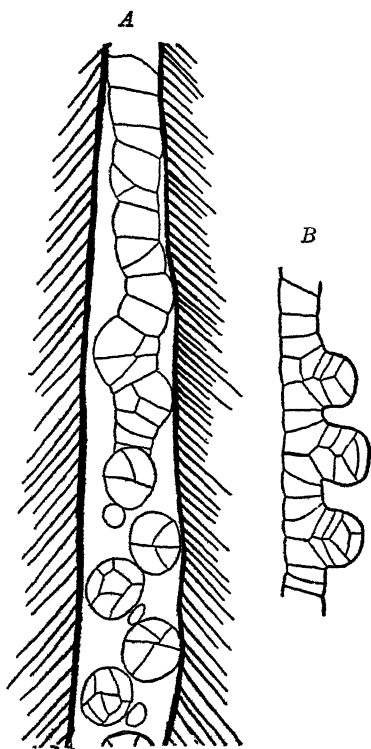


FIG. 305.

Sections from a fertile pinna of *Schizaea digitata*. *A* = tangential section showing the acropetal sequence of sporangia. These are derived from the row of marginal cells, seen at the upper limit of the drawing. The two rows apparent on each side of the adult pinna arise by readjustment during development from the single series of marginal cells. *B* = section traversing the marginal series of cells and the young sporangia vertically. $\times 85$.

But in the Dicksonieae and Dennstaedtiinae various interesting steps are seen illustrating a "phyletic slide" towards the lower surface. A few illustrations will serve to show this. The ancient genus *Thyrsopteris*, with its large sporangia, retains the marginal position of the sorus, while its first sporangium is itself of marginal origin, though succeeded by others of superficial origin (*Ferns*, vol. ii., Figs. 527, 529). But in the allied Dicksonieae, though the first sporangia still arise directly from the marginal series of cells, the whole sorus is deflected towards the lower surface, and increasingly so as it matures. The receptacle is protected on either side by indusial flaps, of which the adaxial is larger than the abaxial (Fig. 306). This inequality becomes more marked in the Dennstaedtiinae, where the adult sori are marginal though turned downwards in *Dennstaedtia*, while in *Microlepia* and *Hypolepis* they may be more or less intra-marginal (Fig. 307, *A*). How this comes about is shown on examination

of the young sorus in longitudinal section (Fig. 307, *B*). The receptacle is then seen to be widely extended and flattened along the vein which bears it. At the basal limit the vestigial lower indusium may still be found (*vi*), while a small rounded lobe seemingly incorporated in the blade as seen in surface view, (*A*), represents the upper indusium (Fig. 307, *B*, *ui*). Such examples seen within a sequence of related Ferns demonstrate a phyletic slide of the marginal sorus to the lower surface of the blade. (For details see *Ferns*, vol. iii., chap. xxxvi.).

Another sequence of the Marginales distinguished from the Dennstaedtiinae by the habitual fusion of its sori, and their slide from margin to surface, is seen in the Pteroid series; it may be illustrated by comparison of the Bracken (*Pteridium*) with the true genus *Pteris*. In the former the receptacle of the marginal fusion-sorus originates directly from the series of

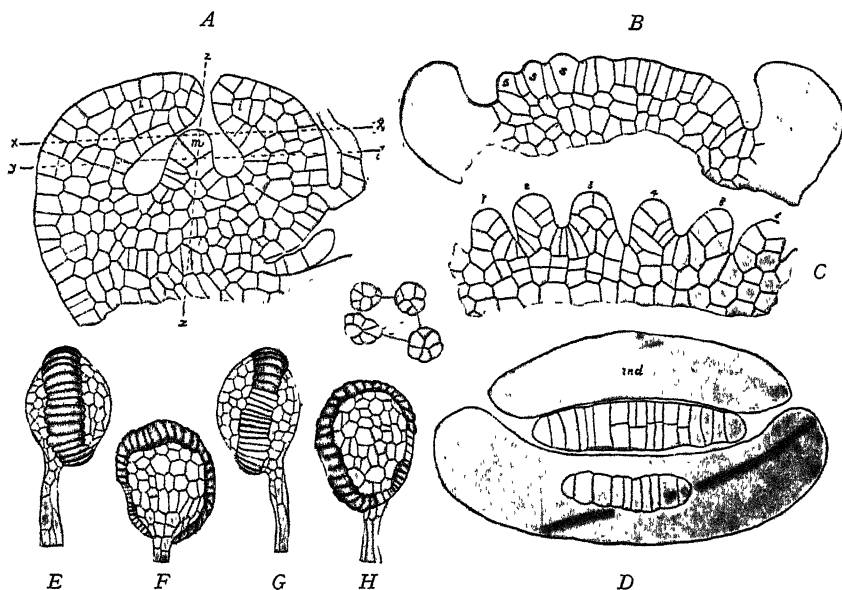


FIG. 306.

Dicksonia Schiedei, Baker. A=section through a young sorus perpendicular to the leaf-surface; *i*, *i*=indusium; *m*=cell of marginal series. B=section of sorus parallel to the leaf-surface as along a line *x*, *z*, in Fig. A, showing receptacle bearing sporangia *s*, *s*. C=a similar section bearing older sporangia. D=transverse section of a young sorus showing the two unequal lips of the indusium (*ind*), and the receptacle between them, as along a plane *y*, *y*, in Fig. A. A section of the receptacle as in plane *x*, *z*, in A, is superposed on the lower indusial lip. The central figure shows sporangial stalks cut transversely. A-D $\times 200$. E, F, G, H sporangia of *Dicksonia Menziesii* from four different points of view. $\times 50$.

marginal cells of the blade, and there is, as in the Dicksonioid series, an upper indusium of stronger development than the delicate lower lip (Fig. 322, p. 388). In the course of development the margin becomes strongly curved downwards, so that the lower indusium is contiguous with the lower leaf-surface, and so becomes functionless. Various stages of its abortion may be observed, and intermediate states of great beauty may be seen in *Histiopteris incisa*, and other Ferns. These lead to the condition shown by *Pteris* itself, in which the upper indusium is still present, but the receptacle, now distinctly intra-marginal, is spread out on the lower leaf-surface, while the lower indusium is obliterated, very much as it is in *Hypolepis* (see Ferns, vol. i., Figs. 218-220).

Such examples as these show the phyletic slide of the sorus from the margin to the lower surface of the leaf in two allied but distinct sequences of

living Ferns. A somewhat similar change has been noted in the quite separate phylum of the Osmundaceae, and it is a general feature though less pronounced in the Schizaeaceae. The results become more accentuated as the individual development proceeds in Ferns now living. Upon such evidence the conclusion is based that *the slide has been polyphyletic* in its occurrence, while the biological advantage of protection during development has been its probable cause. Further, since it has been polyphyletic in

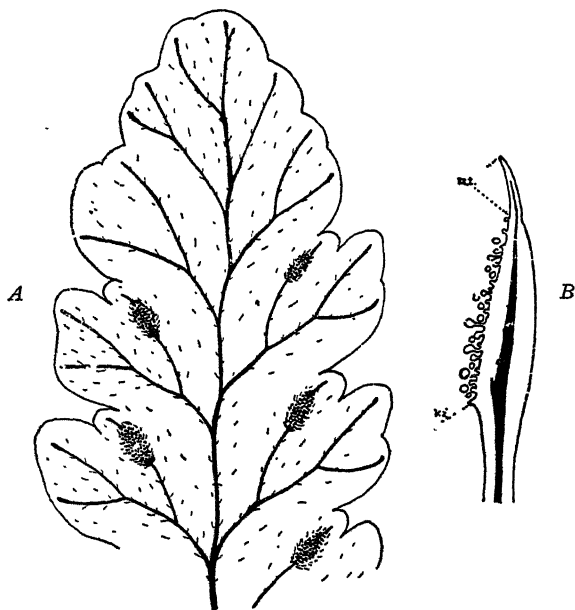


FIG. 307.

A = Pinnule of *Hypolepis repens*, seen in surface view, with sori intramarginal; a small marginal lobe represents the upper indusium. $\times 10$. B = Young sorus of *H. repens*, cut vertically, showing the elongated superficial receptacle. ut = upper indusium; vs = vestigial lower indusium. $\times 15$.

modern Ferns, we may believe that a transition of the sorus from the margin to the surface of the cladode leaf has happened at various times in the evolution of Ferns: that certain families acquired this character as early as the Palaeozoic age—for instance, the Marattiaceae and Gleicheniaceae; while such a type as *Corynepteris*, with its highly-cut Sphenopterid frond, may probably represent an intermediate step towards such superficial sori as are found upon the broader Pecopterid leaves of *Ptychocarpus* (Figs. 296, 301). The general conclusion would then be that the incidence of the "phyletic slide" has not been limited to any one period in evolution. While some phyla of Ferns, to be recognised as *Superficiales*, have carried it out relatively early in descent (Marattiaceae, Gleicheniaceae, Matoniaceae), others, to be designated the *Marginales*, retained the marginal position longer,

and still possess that feature (Hymenophyllaceae, Loxsomaceae, Thyrsopterideae, Dicksonieae); though certain of their derivatives now living give evidence of various degrees of relatively late transition to the biologically more advantageous state of superficial sori (Dennstaedtiinae, Pterioideae).

SUCCESION IN APPEARANCE OF THE SPORANGIA

A. The Simple Sorus

The primitive sporangia of Ferns were relatively few but large, as in those Ferns which have been designated Eusporangiate. Except in so far as there may be some degree of succession, in accordance with the apical growth of the whole part that bears them, those in near proximity upon a leaf or pinna originate simultaneously and develop coincidently. The effect of this is that the physiological drain of spore-production is imposed by all the sporangia at once upon the immediate part which bears them. Such Ferns as show this synchronous scheme have been styled the *Simplices*, a title which includes the Coenopteridaceae, Ophioglossaceae, Marattiaceae, Osmundaceae, Schizaeaceae, and the Matonineae. These are all represented in the Palaeozoic or early Mesozoic rocks: it may therefore be concluded that this condition of the sorus is itself primitive. From a biological point of view the method is certainly very simple, appearing as the result of multiplication of sporangia as units borne upon an enlarging vegetative system, and without regard to the immediate drain imposed upon its nutritive powers. A further result is that at ripeness the whole crop derived from a given part, or even from a whole plant, is shed at the same time. Each spore must take its chance of the conditions being then favourable for germination, or the reverse. Large numbers may increase the chance of success, but this is a wasteful remedy. The introduction of a time-factor into the problem would bring relief from the primitive state of the *Simplices*: and this combined with smaller and more numerous sporangia has largely contributed to the success of the modern Leptosporangiate Ferns over the older Eusporangiate type.

B. The Gradate or Basipetal Sorus

The simple device of increasing the area of the soral receptacle has been fully made use of by the Marattiaceae, especially by *Archangiopteris* and *Danaea*; and they have thereby multiplied both the number of sporangia and the tale of spores while still maintaining the simple type (Fig. 302, *B*, *E*; see also *Land Flora*, Fig. 286). But a similar advantage may be gained by increasing the height of the receptacle, thereby affording greater accommodation in a different way for a larger number of sporangia. Moreover, these need not be produced simultaneously but in succession. Naturally a basipetal succession will be the most practical, so that the youngest shall be

nearest to the source of nutrition, and be protected by a basal indusium ; while the oldest will be most exposed, and the shedding of the spores aided thereby.

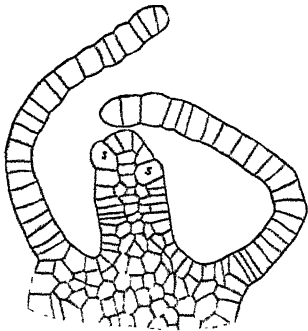


FIG. 308

Hymenophyllum Wilsoni, Hk. Sorus in longitudinal section showing the receptacle with divisions indicating intercalary growth, and the first sporangia originating near the apex. $\times 100$.

The drain of nutrition will by this means be spread over an extended period : and this is the physiological rationale of the *Gradate Sorus*. The receptacle, which may be cylindrical (*Hymenophyllaceae*) or laterally compressed (*Cibotium*, *Thyrsopteris*), possesses in varying degree the power of intercalary growth. Upon it the first sporangia appear at or near to the distal end, and these are followed by a basipetal succession of them (Fig. 308). In later stages the distal sporangia may be found already mature, while towards the base successively younger sporangia may be seen (Fig. 309). This type of sorus is present in the Dicksonieae and Loxsomaceae ; it finds its climax in the Hymenophyllaceae, where the long hair-like receptacle gives the name to the genus *Trichomanes*. These Ferns are all Marginales ; but the Gradate type is also seen in the Cyatheaceae and Onocleinae, where the sorus is superficial (Fig. 315). In them it probably originated from a simple sorus such as that of the Gleicheniaceae. *Lophosoria*, long included in the genus *Alsophila*, is regarded as taking an intermediate place (see *Ferns*, vol. ii., p. 287). The Ferns which bear gradate sori take a middle position in the Class at large, as regards their general characters : and their fossil correlatives date back to the Mesozoic Period. They do not, however, form a phyletic unity. The gradate sorus seems to have appeared sporadically, as a biological adjustment which has affected various lines of descent, whether the sori be marginal or superficial. One further result of the gradate sequence of sporangia upon the receptacle is to raise a difficulty in shedding the spores ; but this is met by the accurate orientation of the sporangia, which are characterised by having as a rule short stalks, an oblique annulus, and lateral dehiscence.

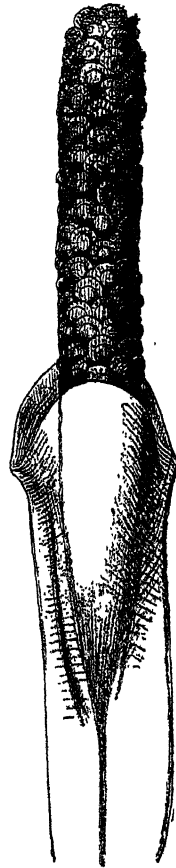


FIG. 309.

Trichomanes tenerum. Sorus in surface view : the placenta bearing radially distributed sporangia, issues from the two-lobed beaker-like indusium, but within the cup-like indusium a basipetal succession of sporangia are enveloped. The annulus is visible on the adult and exposed sporangia. Magnified. (After Goebel.)

The result is that the distal arch of each annulus is free to alter its form independently of the adjoining sporangia, however closely these may be packed together (Figs. 309, 310).

C. The Mixed Sorus

The remainder of the Filicales, which constitute the great majority of the living genera and species, have sori of the type described as "mixed." Here the sporangia are aggregated together without any definite sequence, successively younger sporangia being interpolated promiscuously between those already present. There is no definite orientation of these sporangia, and their stalks are usually long. The annulus is almost always vertical, the dehiscence transverse, and the number of spores per sporangium rarely exceeds 64. The origin of the "mixed" sorus has probably been polyphyletic, and indications of how it came into existence may be drawn from several distinct phyletic lines. For instance, while the Dicksonieae have a marginal and gradate sorus the Davalliaceae have a mixed sorus. The genera *Dennstaedtia* and *Hypolepis* supply the bridge between the two types. In *D. rubiginosa* the receptacle is somewhat flattened, and it bears sporangia of various ages intermixed, though still with a suggestion of a gradate sequence at first (Fig. 311, A). These characters approach those of the fully mixed type of sorus, as seen in *Davallia* (C), where the receptacle is quite flat, and various ages of the numerous long-stalked sporangia are crowded together upon it (Fig. 311, A-C).

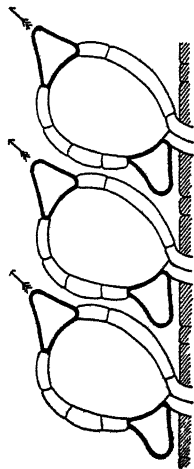


FIG. 310.

Diagram illustrating the relative position of the sporangia on the receptacle in the Hymenophyllaceae. The annulus of each is indicated by heavier lines, and the arrows show the direction of its outward spring.

The *Woodsia-Dryopteris* sequence, with sori not marginal but superficial, gives a second and probably a quite distinct line of progression from the gradate to the mixed state. These Ferns appear to have originated from some Gleicheniaceae source, where the simple sorus was already superficial. The transition to the gradate state is illustrated by *Lophosoria*, *Alsophila*, and *Cyathea*, as already noted. In *Woodsia* there is a minute sorus of this Cyatheoid type; but the receptacle is flat, and there is only a slight indication of a gradate sequence of the sporangia: there is, however, no evidence here of interpolation. But in the shade-loving *Hypoderris*, with its sori dotted over the expanded surface, the type is still Cyatheoid as regards position and indusium, though the numerous long-stalked sporangia arise with their various ages intermixed. The same state appears also in *Diacalpe* and

Peranema, genera which form a natural bridge of transition to the type of *Dryopteris*, which is a typical genus of "mixed" character.

The next point is, however, that all the three soral conditions need not be passed through in arriving at the "mixed" state. A direct transition may be made without any gradate stage. This is seen within the genus *Dipteris*; in which the simplest species, *D. Lobbiana*, has its sori disposed as in *Gleichenia* or *Matonia*, and all its sporangia are of simultaneous origin. But in *D. conjugata*, with broadly webbed leaves and many sori scattered over the surface, a mixed condition is found (Fig. 312). This state is more fully developed in such

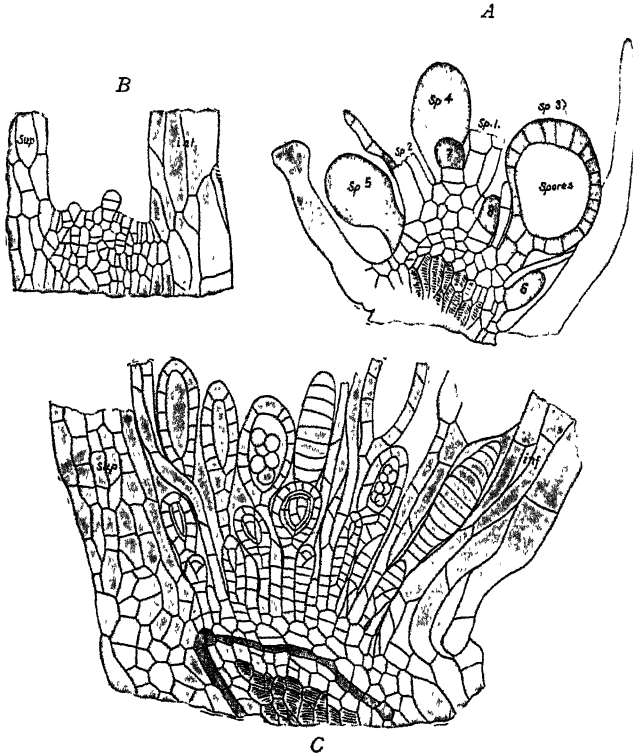


FIG. 311.

A=sorus of *Dennstaedtia rubiginosa*. Cut vertically and showing mixed condition of a sorus originally basipetal. B=*Davallia Griffithiana*, Hk. Young sorus in section, showing first formation of sporangia. C=old sorus of the same, showing sporangia of different ages intermixed. All $\times 100$.

derivative genera as *Cheiropleuria* and *Christopteris*. It is probable that *Neochheiropteris* and even *Phlebodium*, with their widely extended and mixed sori, also sprang from the simple Dipteroid stock. If this be admitted then the following general progression would illustrate the origin of a mixed sorus directly from a simple, superficial source: viz., *Gleichenia* or *Matonia*: *Dipteris*, *Cheiropleuria*, *Christopteris*: and finally *Neochheiropteris*, and that section of the old genus *Polypodium* which is included under the name

Phlebodium (Fig. 313). Yet another series giving a like result is found in the Gymnogrammoid Ferns with their ill-defined and mixed sori, which are probably traceable from the superficial *Todea*, through such genera as *Llavea*,

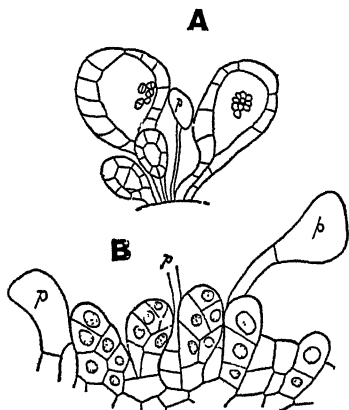


FIG. 312.

Dipteris conjugata. A=section of a young sorus showing sporangia of different ages in juxtaposition. $\times 100$. B=younger sporangia; p =paraphyses. $\times 300$. (After Miss Armour.)

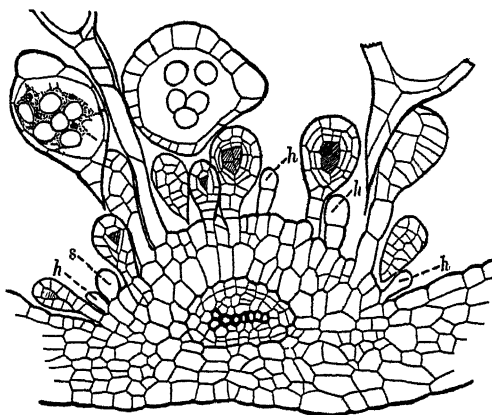


FIG. 313.

Young sorus of *Polygodium* (*Phlebodium*) *aureum*, L., cut vertically. Showing sporangia of various ages intermixed. s =sporangia. h, h =hairs.

Plagiogyria, and *Cryptogramme*. There is thus sufficient evidence to suggest that there has been direct, polyphyletic progression from a simple to a mixed sorus; and that the gradate stage, though existent in certain lines, is not a necessary step towards the attainment of a mixed sorus.¹

PROTECTION OF THE SORUS

In all Ferns protection of the spore-producing organs is given in the first instance by the juxtaposition of parts in the young state; and particularly by the circinate vernation, a feature already present in Devonian fossils such as *Asteroxylon*, or *Psilophyton* (Frontispiece). In the Ferns the distal end of each leaf is enfolded while young within the older parts: and this has special importance in view of their continued apical growth. The lower and older parts are successively exposed as the leaf unfolds, and this may help to explain the frequent absence of sporangia in its basal region. *Osmunda regalis* is an example of this, and it is a common feature in *Dryopteris*. But in addition to such general protection as this, special developments of the most various kind, serving a like end, appear in relation to the sorus. When these take definite form they are included under the general name of *Indusium*. But since such protective organs originate, as we shall see, in various positions, and spring from divers sources, the term indusium cannot connote any

¹ *Ferns*, vol. ii., chap. xxxiv.; vol. iii., chap. xlv.; Figs. 716, 725.

definite morphological entity : the word is in fact used in a general descriptive sense.

The Simplices form their sporangia simultaneously, and initiate them early ; this fact, and their usually massive character, makes the need for their protection less urgent than in the Gradate and Mixed types, with their succession of more delicate sporangia. Hence the usual absence of special protection in the Simplices : a few hairs round the base of the sorus in *Angiopteris* or *Marattia*, or a partial sinking of the sori into the tissue of the blade in *Danaea*, suffices for them in addition to the circinate vernation. In *Marattia*, *Danaea*, and *Ophioglossum* there is also mutual protection of the sporangia by their fusion to form synangia. In *Helminthostachys*, however, definite growths are seen occasionally at the distal ends of the sporangio-phores, and these form an imperfect covering ; but a much more efficient organ of protection of like nature appears later in *Matonia*, shielding the sporangia like an umbrella. Such rudimentary growths may be ranked with those indusium-like processes which accompany the sporangial groups in *Botryopteris antiqua* ; and collectively they suggest that protective structures may have originated sporadically among early Ferns, though many of these are without them ; and that the latter is the primitive state.

In their upward evolutionary lines the Leptosporangiate Ferns have shown variety and resource in the methods of protection of their sporangia, the diminishing size of these making them more vulnerable to exposure than those of the Eusporangiate Ferns. In the position of the sori two main evolutionary lines have been recognised, viz., the Marginales and the Superficiales, distinguished respectively by the degree of retention of the originally marginal stance of the sorus, or of its relatively early transference to a superficial position. The former may be traced from a Schizaeoid source, the latter from a Gleichenioid. A wide comparison based on fossil and living types, points to the conclusion that not only have these two lines been historically distinct from very early times, but also that such indusial developments as they show have originated along distinct channels. Nevertheless they have approximated in form, so that the indusia of certain of those Marginales in which the sori ultimately passed to a superficial position closely resemble those of the Superficiales, in which the position of the sorus on the lower surface was assumed early in descent. Here the sori of the two sequences will be described separately, and the probable origin of their indusia traced.

The Schizaeaceae are a very distinctly synthetic family of Ferns : in particular their relation to indusial development is very suggestive for comparison with other *marginal* types. It has been seen that their sporangia all originate singly from the marginal series of cells of the cladode leaf, and protective growths of various form spring up below the individual sporangia. In *Lygodium* the protection takes a pocket-like form, which envelops the

marginal sporangium, extending to both surfaces of the blade (Fig. 304, *B*). Its origin has been traced as superficial, not marginal, and at first it appears as a uniform and continuous flap (Fig. 314; also Fig. 304, *C*). As it matures the pocket differentiates into an upper (adaxial) and lower (abaxial) lip; the first is massive, appearing as though it were a continuation of the blade of the leaf-segment, the lower lip becomes membranous: together they enclose the monangial sorus. In other genera of the Schizaeaceae the protective flap may take other forms (Fig. 304, *D*, *E*, *F*), but in all of them its function is the same, while its strong growth from the upper surface tends to thrust the marginal sporangium which it covers towards the lower surface.¹ The name of indusium has been applied to this organ, and that of *Lygodium* may be accepted as suggesting the origin of that form of two-lipped indusium which has prevailed along the whole line of the *Dicksonia-Davallia-Pteris* series of

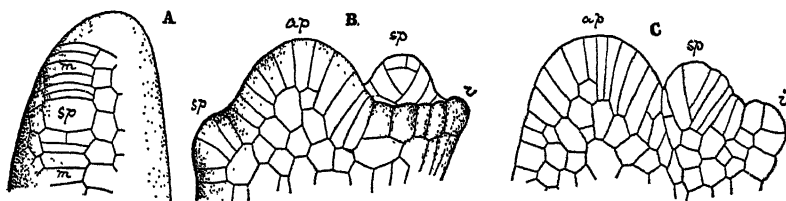


FIG. 314.

Origin of the marginal, "monangial," sorus of *Lygodium*. *A*=margin of young pinnule in surface view; *m*=marginal cells; *sp*=sporangium. *B*=a similar pinnule in surface view; *ap*=apex; *i*=indusium. *A* and *B* after Prantl. *C*=the same seen in section. (After Binford.)

the Marginales. In the Loxsomaceae and Hymenophyllaceae the indusium is, however, cup-like, or only faintly lipped. In all of the Ferns named the indusium is of basal origin, involving upgrowth from the intra-marginal surface of the blade.

The step from the *Lygodium*-type to a *Dicksonioid*-type of sorus is but a slight one. Given an initial series of marginal sporangia, followed by a gradate sequence of those later developed upon the receptacle, and a more massive structure of the superficial indusial flaps, the relations are comparable with those of *Lygodium* (Figs. 306, 314): and this will apply for the whole sequence of the Marginales. But in the course of their evolution changes may appear in the position, structure, and even in the persistence of the constituent parts. The Loxsomaceae, Hymenophyllaceae, and Thyrsopterideae retain the marginal position of the sorus most perfectly, and with this goes the completion of the indusial ring surrounding the cylindrical and gradate receptacle (Fig. 309). But in the *Dicksonieae* the sorus tends towards the lower surface, with an inequality of the indusial lips already foreshadowed in *Lygodium* (Fig. 306). The phyletic slide of the sorus to the lower surface of the blade is accompanied by an advance to a "mixed" state in *Hypolepis*,

¹ *Ferns*, vol. i., Figs. 213, 214.

and in the Pteroid Ferns generally, and by the abortion of the lower indusium; meanwhile the upper may be apparently merged in the flattened blade, sometimes being recognisable as a minor marginal lobe (Fig. 307). In *Pteris* itself the transition (which may be traced with most gradual steps in *Histiopteris incisa*), is complete, and the upper indusial flap merges into the margin of the blade, while the lower has disappeared.¹ But it is still present in a vestigial state in the Bracken, though it can be of little use for protection where the sorus is closely appressed to the lower leaf-surface (Fig. 322). Thus the end-result reached, partly along lines of comparison, partly by

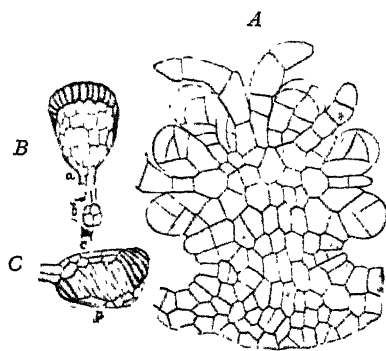


FIG. 315 A.

A = *Alsophila atrovirens*, Presl. A young sorus cut vertically, and showing a slight indication of basipetal succession of the sporangia. There is no indusium. $\times 200$. *B*, *C* = sporangia of *A. excelsa*, Br. Mature; *b* = a transverse section of a sporangial stalk. $\times 50$.

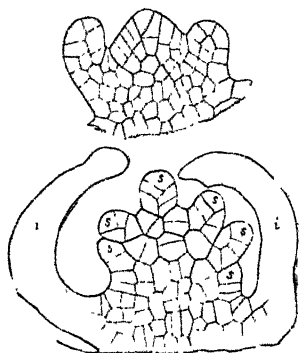


FIG. 315 B.

Cyathea dealbata, Sw. The upper figure shows a very young sorus, with receptacle and indusium already indicated. The lower shows the indusium (*i*) more advanced, and the sporangia *s*, *s*, arising in basipetal succession. $\times 200$.

ontogenetic and vestigial evidence, is that of an apparently superficial, non-indusiate, mixed sorus, a state very different from the marginal and monangial sorus of the Schizaeaceae.

Passing now to the Simplices with *superficial* sori, the ancient Marattiaceae and Gleicheniaceae are without any definite indusium. But among the Gradatae there are Ferns with sori in the same position, some without and some with a basal indusium. The question then naturally arises whether the indusium is here homologous with that of the Marginales, such as the *Dicksonia-Davallia-Pteris* series; or is it of independent origin within the Superficiales, as represented by such genera as *Gleichenia*, *Lophosoria*, *Alsophila*, *Woodsia*, *Hemitelia* and *Cyathea*? The immediate question as to the origin of the indusium of these Superficiales turns upon the well-assured fact that the Ferns named have existed as a consecutive phylum from early Mesozoic or even Palaeozoic times. A representative sequence for comparative purposes may be seen in these living genera, while the Woodsieae lead on through *Diacaalpe* and *Peranema* towards the Dryopterid Ferns. If no Ferns existed

¹ See *Ferns*, vol. i., Fig. 219.

other than those named the natural inference would be that they illustrate the origin of a new and efficient organ of protection, viz., the "*indusium inferum*" (Fig. 315). *Gleichenia pectinata* and *Lophosoria* are Ferns with dermal hairs only, and no scales: hairs are found associated with the

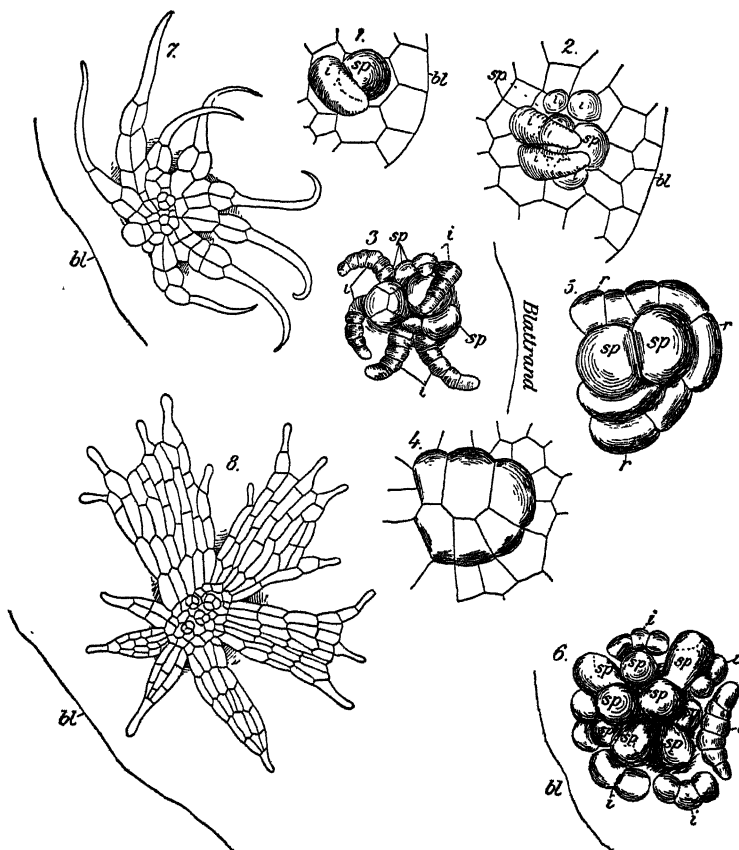


FIG. 316.

1, *Woodsia ilvensis*, young sorus with sporangium (*sp*) and indusial hair (*i*). 2, later stage of same. 3, ditto, older. 4, *W. obtusa*, very young receptacle. 5, ditto, with sporangia (*sp*), surrounded by the ring-like indusium. 6, ditto, older stage. 7, *W. ilvensis*, mature indusium; *bl* = leaf-margin. 8, *W. obtusa*, mature indusium and leaf-margin (*bl*). (After Schlumberger.)

sporangia in their simple and naked sori. *Alsophila* and *Cyathea* have dermal scales, and these genera show successive steps in perfecting the inferior cup-like indusium, while in the Woodsieae traces of a parallel sequence are found in their fimbriated inferior cups, which suggest an upward construction from primitive constituent hairs (Fig. 316). In *Cyathea* the sorus is radially constructed. But in *Hemitelia* the cup is deficient on the side next to the margin of the pinnule, as it is also in *Woodsia*. In *Peranema* this is combined with a lopsided development of the whole receptacle; in *Dryopteris* the lopsidedness

is more pronounced, and the sequence culminates in the peltate "*indusium superum*" of *Polystichum*. The last step of all in this series is a partial or complete abortion of the indusium, giving the Polypodioid state seen in the native Oak and Beech Ferns. Biologically it may be noted that the most perfect protection is in the gradate tropical genera.

The general inference from these comparisons will be that the indusium of the Superficial Series, which starts with a naked sorus present in Palaeozoic times (*Oligocarpia*), illustrates an upward origin of soral protection, founded on soral hairs (*Gleichenia*, *Lophosoria*), and that these coalesce or widen to a partial or complete basal cup in those genera which bear dermal scales (Cytheaceae and Woodsieae). From these, by steps generally accepted, the

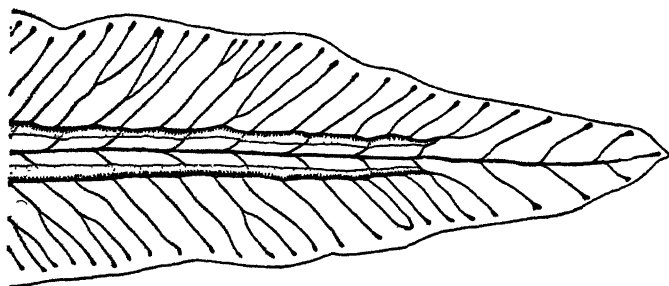


FIG. 317.

Blechnum longifolium. $\times 3$, showing the relation of the fusion-sorus to the venation, and its protection by a continuous "indusium" which is phyletically the leaf-margin folded downwards. The expanded leaf-surface is here a new formation, which has the effect of increasing the photosynthetic area.

reniform and peltate indusia of the Dryopterids were derived. The facts have, however, been read in reverse by Schlumberger, who regards the indusium of *Woodsia* as in process of dissolution into constituent hairs (Fig. 316, 7, 8). He does not appear to have reckoned with the fossil story. Unless the whole series of the Superficiales, from *Oligocarpia* to the living Ferns, is to be read in reverse, the opposite view seems justified: viz., that the *indusium inferum* originates from dermal appendages, and is distinct in evolutionary origin from the indusia of the Marginales. The two types of indusium would consequently be homoplastic not homogenetic parts, though both are of the general character of "enations" (see Chapter XXX). These are only two out of a plurality of sources from which the soral protection has sprung in the Ferns at large.¹

A further type of protection is seen in the genus *Blechnum*, where the fertile pinna shows features difficult of explanation, unless its development be studied comparatively. Seen from below it appears as in Fig. 317, as a flat photosynthetic expanse with a central midrib, on either side of which runs a

¹ For a full discussion of the "*indusium inferum*" reference may be made to *Ferns*, vol. iii., pp. 114-118.

continuous incurved “*indusium marginarium*” (Presl): this covers a continuous coenosorus. Comparison with *Blechnum*, *Lomaria*, and finally with

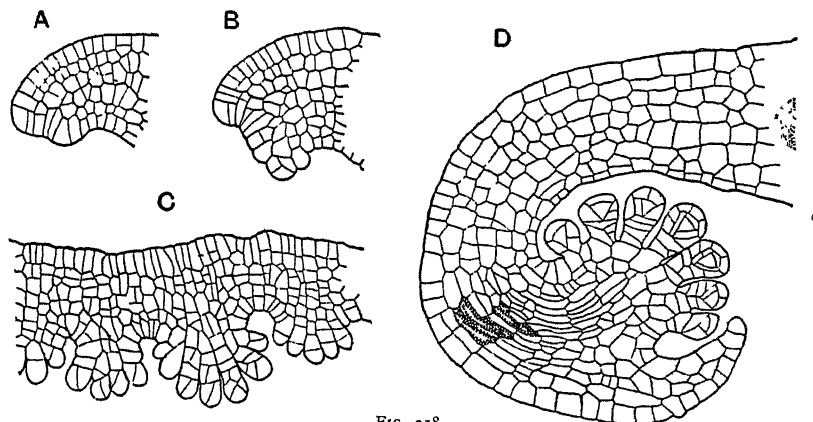


FIG. 318.

Development of the sorus of *Matteuccia intermedia*. A, B, D=sections through the pinna-margin showing successive stages of the superficial, gradate, non-indusiate sori, protected only by the curved margin. C=a section parallel to the margin, traversing a succession of distinct non-indusiate sori. $\times 125$.

Matteuccia gives a basis for the interpretation of this unusual structure. In the latter genus the margins of the fertile pinnae are strongly curved downwards, covering the linear series of gradate exindusiate sori, which are like those of *Alsophila* in structure and position, thus suggesting a Cyatheoid

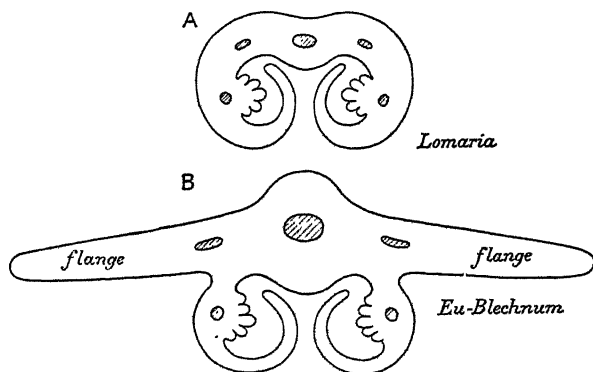


FIG. 319.

A=diagrammatic section of the fertile pinna of the type of *Lomaria*, with incurved margins, but no flange. B=a similar section of the type of *Eu-Blechnum*, showing the same parts as before, but with the addition of flanges right and left. Compare Fig. 317.

ancestry (Fig. 318); the sterile pinnae are wide and flattened. In the related genus *Onoclea* each sorus has a membranous indusium comparable with that of *Hemitelia*; in both it probably represents a ramentum. If the sori of *Matteuccia* were fused in linear series the result would be like that actually

seen in *Lomaria*, the pinna-margin covering the coenosorus like a continuous indusium. But this would be photosynthetically inefficient. In *Eu-Blechnum* comparison of the numerous species leaves no doubt that a new formation has arisen on each side along the lines of greatest curvature of the convex surface. It takes the form of a flange right and left, and is supplied with vascular strands similar to those of the normal sterile pinnae (Fig. 319). Here what is usually described as the indusium is really the incurved margin.

Lastly, additional protection, beyond that of the crowded sporangia themselves, may be given by hairs distributed through the soral area, particularly where the receptacle is flattened over the surface of the exposed sporophylls. The hairs may branch freely (*Metaxya*, *Niphobolus*, *Platy-cerium*), and are sometimes peltate (*Polypodium piloselloides*, *Drymoglossum*), sometimes glandular (*Vittaria*, *Acrostichum aureum*). Occasionally they may be borne on the sporangia themselves, as in *Polypodium crassifolium*. These are all in their degree effective protections, and may serve as a diffused indusium, particularly to the smallest and youngest sporangia in a mixed sorus. The cumulative effect of comparison thus shows that the methods of protection of the developing sorus are very various, and this strengthens the view that those methods have been widely polyphyletic.

INDIVIDUALITY OF THE SORUS

The sorus consists of a compact group of constituent parts: viz., the receptacle with its vascular supply, the sporangia, and the indusial flaps. It appears in so many Ferns to be strictly circumscribed that it may readily be looked upon as a morphological entity. This view seems to be accentuated by the changes in its position already described. Its apparent individuality is based upon nutrition: the limited outline marks a convenient radius of nutrition-supply from a vein, marginal or intra-marginal. Historically the existence of the single distal sporangium of *Stauropteris* (Fig. 294), or of the tassel of sporangia in *Etapteris* (Fig. 295), condensed to the state seen in *Corynep-teris* (Fig. 296), support this view; allowance being made for the adoption in more advanced Ferns of a gradate or mixed sequence of the sporangia, and the addition of indusial protection. But if convenience of nutrition be the real cause, then it may be expected that a bifurcation of a vein may by *fission* support twin sori; or that a fusion of veins, as seen so commonly in the later reticulate Ferns, may be associated with soral *fusion*, to form *coenosori*; or these again may break up into fragments in case the vascular connection be again interrupted. All of these states can be illustrated among the more advanced types of living Ferns, showing that the sorus is not itself a morphological entity for Ferns at large.

A relatively primitive state was doubtless that in which a narrow leaf or segment bears a single row of sori on either side of the midrib. This is

characteristic of the Gleicheniaceae, Hymenophyllaceae, and Dicksonieae. If the photosynthetic leaf widens the sori may extend with it, as in *Danaea* or *Archangiopteris* (Fig. 302); but this may lead to fission of the sori, occasionally seen in *Danaea*, culminating in the state normally present in *Christensenia* (Fig. 320). The like occurs also in *Dipteris* and *Metaxya*.¹ Thus it

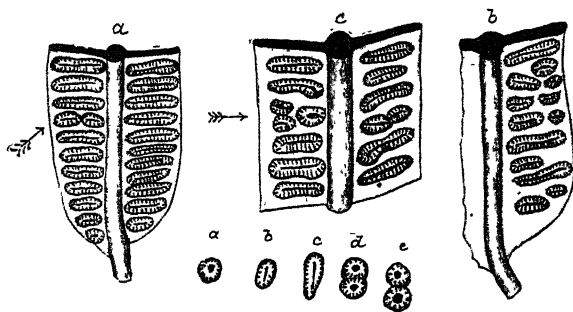


FIG. 320.

a, b, c (above), *Danaea alata*, Smith. *a*—a fertile pinna with many normal sori: the arrow indicates an abnormal fission; *b, c*, show more numerous abnormal fissions, resulting in irregularly formed sori, distributed over a slightly enlarged leaf-surface. $\times 2$. *a, c* (below), sori of *Christensenia aesculifolia* (Bl.) Maxon, showing states of partial or complete abstriction.

appears that the individuality of the sorus may be lost by *fission*. On the other hand, where sori are crowded their individuality is apt to be lost by *fusion*, especially where they are borne in linear sequence. For instance, in *Saccoloma*, *Nephrolepis*, and *Lindsaya* various stages of linkage of the sori may be seen (Fig. 321); and the fusion-sorus becomes typical for *Pteris*. In

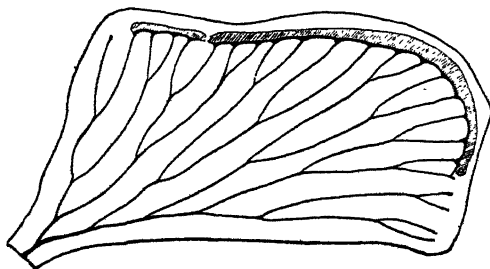


FIG. 321.

A single pinna of *Lindsaya lancea*, showing the sori fused laterally to form an almost continuous intra-marginal series. $\times 4$.

this feature the Bracken (*Pteridium*) occupies an interesting position (Fig. 322). The coenosorus is here strictly marginal in origin, the receptacle springing from the marginal series of cells (*x, A, B*). The sequence of sporangia, though sometimes basipetal as in the variety *caudatum*, is usually mixed: the indusial lips are of superficial origin as in the Dicksonieae, but the lower is often vestigial. In all of these features the Common Bracken is of

¹ *Ferns*, vol. i., Figs. 222, 223.

the Dicksonioid type: the difference chiefly lies in the soral fusion to form marginal coenosori. This is based upon vascular commissures linking together distally the vein-endings, which are normally free in the sterile parts (Fig. 322, C). The indusia then form continuous protective flaps, while the sporangia of various ages are crowded along the length of the continuous receptacle. The quite distinct sequence of the Blechnoid Ferns affords a similar result, but the structural details as explained above are quite different (Fig. 317, p. 384).

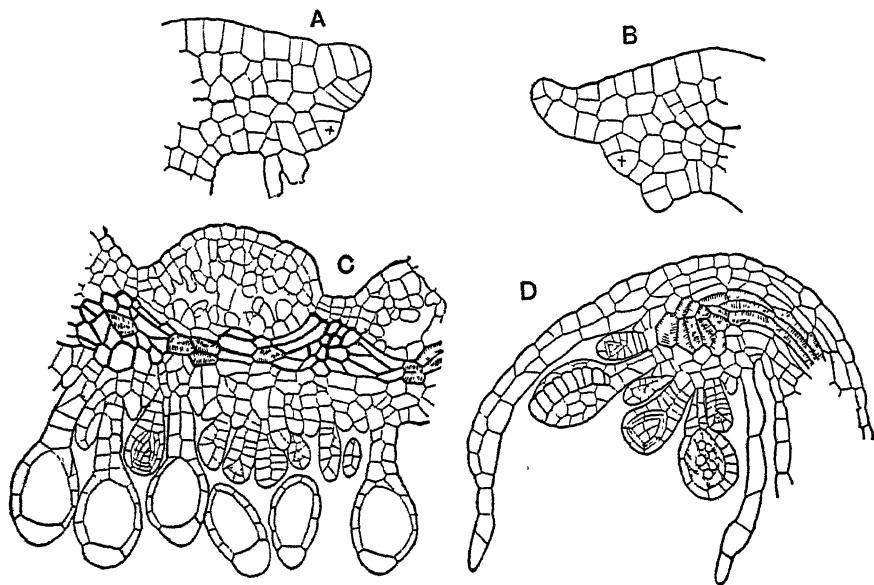


FIG. 322.

A, B=vertical sections through the margin of the pinnule of *Pteridium aquilinum*, showing how the receptacle (z) originates directly from the marginal segmentation, while the indusial flaps are of superficial origin. $\times 180$. C=vertical section of the fusion-sorus, following the line of the vascular commissure. $\times 90$. D=section of a more mature sorus than in A and B, but in a similar plane. C and D show the mixed character. $\times 90$.

The last-named sequence provides instances of a converse progression, viz., in *disintegration of the fusion-sorus*. The result may be a number of partial coenosori disposed in two rows corresponding in position to the undivided type, but not to its originally constituent sori. This becomes the leading feature of the genera *Woodwardia* and *Doodya*. Various steps in a like interruption of the coenosori may be seen in *Blechnum punctulatum*, var. *Krebsii*, and it is there associated with an expansion of the leaf-surface and outward arching of the coenosori (Fig. 323, A-D). This state, combined with extreme expansion of the undivided blade, leads to the condition characteristic of the Hart's Tongue (*Phyllitis scolopendrium*, Fig. 323, E). It would be difficult in this extreme form to trace the identity of the sori from

which by comparison it is concluded that the fertile tracts have sprung. Such examples as these fully demonstrate the merging of the individuality of the constituent soral units.

Finally, the soral unit may be completely merged in that state which is described as non-soral or Acrostichoid. A good example is seen in *Leptochilus cuspidatus*, representative of the Dryopteroid Ferns (Fig. 324). Here

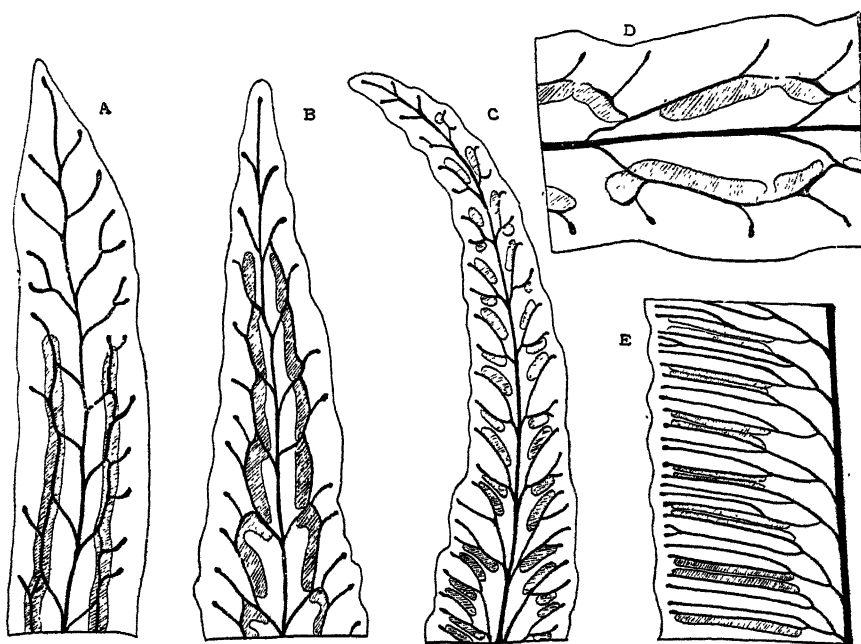


FIG. 323.

Drawings illustrating the disintegration of the Blechnoid fusion sorus (shaded), and its relation to the venation. A = *Blechnum boreale*. B, C, D = *Blechnum punctulatum*, var. *Krebsii*. D = part of the same drawn on a higher scale to show stages of partial disintegration. E = *Scolopendrium vulgare* (= *Phyllitis scolopendrium*), for comparison. A, B, C, E slightly enlarged. D $\times 6$.

the indusium is absent, and the sporangia, as though set free, are spread generally over the surface of the fertile but attenuated blade. The Ferns which share this feature were all assembled by the earlier systematists into the nominal genus *Acrostichum*. It was not recognised by them that that state might be attained along a plurality of evolutionary lines. It remained for later analysis to show that the incongruous group which were brought together under the lax diagnosis of the old genus should be broken up, and the several types allocated to their various natural affinities which are now based on other characters than the mere dissolution of the sorus. The realisation of this has resulted in the whittling away of an unnatural grouping, till all that remains of the old unwieldy genus is the widespread tropical

Acrostichum aureum, and one or two others, which are now recognised as Pteroid derivatives. The justification for this reference is found in the anatomy, habit, and venation, and particularly in the steps of spread of the coenosorus, as seen in *Acrostichum praestantissimum* (Fig. 325). At the distal end of the leaf of this species the sorus differs little from that of *Pteris podophylla* (a), while the venation is the same. But sections lower down show gentle steps of spread of the sorus inwards (b, c), leading towards the complete covering of the lower surface, as it is in *Acrostichum aureum*, which in anatomy is characteristically Pteroid. Following similar lines of wider observation and argument it may be concluded that *Syngramme* and *Elaphoglossum* should be referred to the Metaxyeae; *Trismeria* to the Gymnogramminae; *Brainea* to the Blechnae; *Cheiropleuria*, *Christopteris* and *Platycterium* to the Dipteridinae. Thus it appears that a wide polyphyletic origin may be ascribed to that state which has been called Acrostichoid.

It is not only *Acrostichum*, however, which has needed to be thus combed out into the various phyla, the "Acrostichoid" derivatives of which were formerly associated together as the

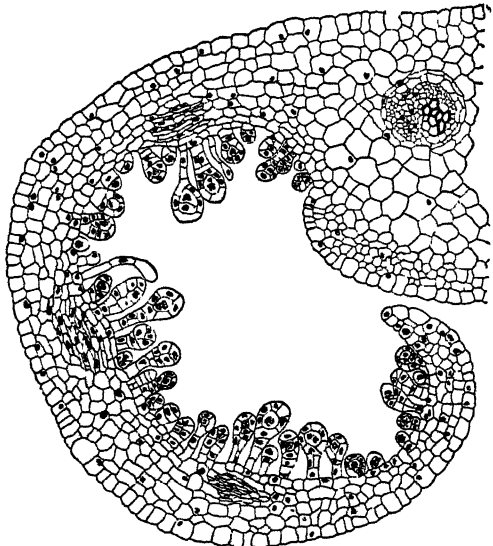


FIG. 324.

Leptochilus cuspidatus. Young sporophyll in transverse section, showing the Acrostichoid state. × about 55. (After Frau Eva Schumann.)

logical outcome of a too indefinite diagnosis. Further examples are seen in *Polypodium*, based upon superficial sori more or less circular in outline, without any indusium; or *Gymnogramme*, also with superficial sori, but linear or oblong, simple or forked, arising from the veins, and again without indusium. In neither of these does the old diagnosis distinguish between primitively non-indusiate types and those which became so by abortion of a pre-existent indusium; consequently *Polypodium vulgare*, in which there is no evidence that an indusium ever existed, is grouped with the Oak Fern, *Dryopteris Linnaeana*, C. Chr. (*Polypodium Dryopteris*, L.), which is clearly "Polypodioid" only by obliteration of the indusium; or, again, *Gymnogramme leptophylla*, Desv. (= *Anogramme*, Link), in which there is no evidence of any pre-existent indusium, is grouped with *Gymnogramme Pozoi*, Kunze, which, like the native *Ceterach*, is an *Asplenium* with an obsolete

indusium. There is no need to multiply examples. The point is that so long as the systematic arrangement of Ferns is based primarily upon sori and sporangia, a more exact diagnosis of genera must follow on increase of detailed knowledge, and in this a wider basis must be found for comparison, and its attendant systematic grouping. But the result will inevitably be to disintegrate still further the old and more comprehensive genera, and to comb them out into better accredited evolutionary lines. This is not a systematic work, so there the matter will be left. It must suffice to have indicated where the methods of the older systematists are out of accord with later evolutionary views.

In the preceding pages sufficient has been stated to show that in the more advanced Leptosporangiate Ferns the sorus has proved very plastic: so much so that it cannot always be accepted as a stable morphological entity, though it probably originated in them all as a condensed branch-system of fertile twigs, in fact as a "telome-truss." It is also apparent that its changes, whether of position, of constitution, of fusion, disintegration, or of spread

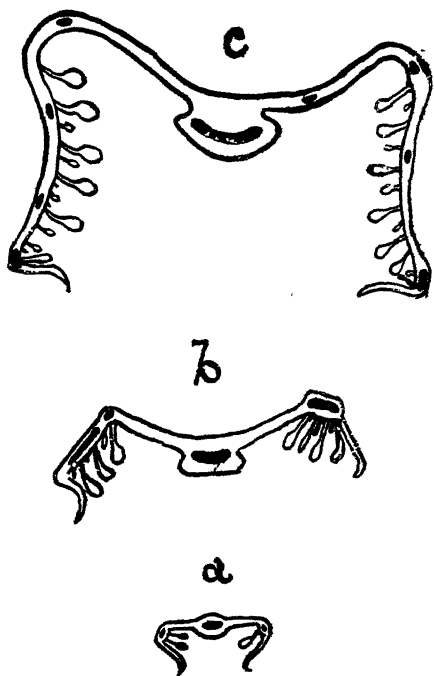


FIG. 325.

a-c=successive sections of a pinna of *Acrostichum praestantissimum*, Bory, from the apex downwards, showing the gradual widening of the Pteroid sorus inwards from the margin. $\times 20$.

over the leaf-surface, have been carried out along polyphyletic lines, each of which is susceptible of an organographic interpretation. There is no reason for wonder that the systematic grouping of these plants, so far as it has been based upon soral characters, has led to great differences of opinion. These find their reflection in that perplexing synonymy that has dogged the steps of Pteridologists. We now see that this difficulty has in large measure originated from defective systematic method; and in particular from diagnoses based on a single feature. This practice, however useful as a means of methodical arrangement of species with a view to record, reference, and naming, cannot possibly lead to a Natural Classification of so complex a Class as the Filicales. To achieve this all available features should be brought into use in diagnosis.

CHAPTER XIX

THE SPORANGIUM OF THE FILICALES

A. THE PALAEOZOIC TYPE¹

THE essential feature of a sorus, stripped of all its variants and accessories, is the *Sporangium*. This spore-producing unit was antecedent in origin to all soral development, dating back to the earliest steps in the evolution of vascular plants; it may even be that a still earlier correlative existed in the isolated sporogonial head of some simple type of Bryophyte, representing an original "Telome." Within the Class of the Filicales the sporangia present differences in number, size, and structure, and in productive power which may be roughly measured by the numerical spore-output of each. These features will be treated comparatively in relation to those of the vegetative system that bears them. The outcome of such comparison shows that parallel progression has taken place not only in respect of one feature or another, vegetative or propagative; but that, as we proceed from types which the fossil record proves to have been of early occurrence to those of later appearance in evolution, there is a general uniformity of progression in respect of them all. As seen in the Ferns this leads from a more massive and less specialised state of the whole sporophyte to one of finer and more highly specialised structure. But it is more clearly reflected in the sporangium than in any other part, a fact which testifies to the prescience of the early writers who fixed upon that part as the basis of their systematic treatment. A careful description of the details of sporangial structure is therefore necessary. It will start from selected examples of the Eusporangiate Ferns which were relatively early in appearance in the fossil record, and are massive in form; and it will proceed to the more delicate and highly specialised Leptosporangiate Ferns of the present day.

In the preceding Chapter the solitary sporangium of the ancient fossil *Stauropteris* has been described, with its vascular stalk, massive wall, and distal pore giving exit to the numerous spores (Fig. 294). But here no

¹ For citations of Literature refer to footnote to heading of Chapter XVIII. See also **Russow**, *Vergleichende Untersuchungen*, 1872, p. 87, who here first used the method of spore-counts; and to **Bower**, *Origin of a Land Flora*, where that method was extended, p. 642; also **Halle**, *Arkiv. für Botanik*, Bd. xvii., 1921, and **Hamshaw Thomas**, *Proc. Camb. Phil. Soc.*, 1922, p. 109, who used the method in comparison of fossils. For a full citation of relative Literature see **Bower**, *Ferns*, vol. i., chap. xii., and vol. ii., chaps. xviii.-xxvi.

mechanical aid to dehiscence has been noted. The nearest approach to this simple type among living Ferns is seen in *Botrychium*, in which also the position of the capsule is terminal, though on a very short pedicel, while there is no specialised mechanism that aids dehiscence, which is by a distal slit (Fig. 299, C-E). The origin of the sporangium is "eusporangiate," by the outgrowth of a number of cells (Fig. 326, A). The sporogenous tissue normally springs from a single cell in a median position, which soon undergoes

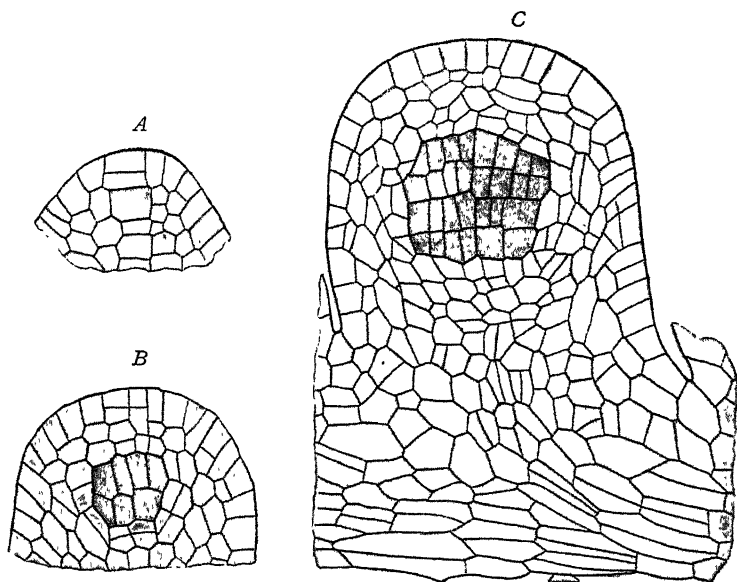


FIG. 326.

Stages in development of the sporangium of *Botrychium daucifolium*. A, B=early stages which show that the sporogenous tissue (shaded) originates from a single hypodermal cell. In C the sporogenous tissue is more advanced, while there are indications of the origin of a vascular strand traversing the massive stalk. $\times 200$.

periclinal division; the inner cell produces by repeated cleavages (B) a well-defined block of sporogenous tissue (C). The sporangial wall meanwhile has become many-layered, while elongated procambial cells traversing the short stalk mark the course of the vascular strand. This has been traced in a mature state as ending in diffuse tracheides immediately below the spore-cavity. Such structural details are important for comparison with *Stauropteris*. The results in *Helminthostachys* are substantially the same (Fig. 300, E, F). The fertile tract in either case is surrounded by an ill-defined tapetum: the same is seen also in *Ophioglossum*. The sum of these details, as seen in the mature state, points to a very primitive type of the Ophioglossacean sporangium, while the similarity to what is seen in *Stauropteris* suggests that they all represent types of early date. The spore-output is large: it may vary from 1000 to 2000 in *Botrychium*; but in *Ophioglossum*

it may be larger, and in *O. pendulum* estimates reach a figure of 10,000 or more from a single sporangium.

The leaves of the Ophioglossaceae may all be interpreted as condensed cladodes, of which certain portions retain fertility, the sporangia being distal upon the ultimate branchlets. *Botrychium* lends itself most easily to that interpretation. The venation of the sterile blade is dichopodial, and that of the fertile twigs is the same. An examination of their tips will make clear the relation of each sporangium as distal on its own vascular branch (Fig. 327); moreover, the slit of dehiscence is actually distal and vertical. Though the sporogenous tissue of each normal capsule originates from a single archesporial cell

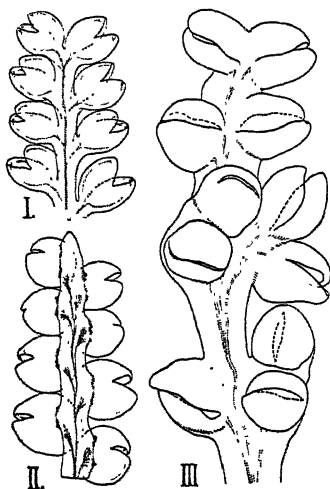


FIG. 327.

Fertile pinnules of *Botrychium*. I.—*B. virginianum* from below. II.—*B. obliquum* ditto. III.—*B. simplex* from above. $\times 6$. (After Von Goebel.)

the identity of the sporangium thus constituted is not always maintained: two or more may appear occasionally as though coherent together. Developmentally this is the result of a partial fission of the sporogenous mass, and various intermediate states may be found either in *B. Lunaria* or *daucifolium* (Fig. 298, D, G). This suggests incomplete forking of the fertile branchlet, of the same type as has been seen in *Hornea* (Fig. 441, p. 593), both being referable to dichopodial branching of fertile twigs.¹

The fertile spike of *Ophioglossum*, with its two lateral rows of sporangia, may best be brought into line with that of *Botrychium* by the suggestion of further condensation, together with lateral fusion, and probably also fission, of the sporangia, so as to form synangia (Fig. 244). It is true that the vascular supply, which consists of strands springing from the complex system of the midrib in *Ophioglossum*,

traverses each septum dividing the closely set sporangia (Fig. 328). This course, as seen in *O. vulgatum* or *reticulatum*, does not readily accord with such a theory of fusion; but in the relatively simple spike of *O. peduncululosum* each strand may show an apparent relation to a pendent sporangium.² Questions such as this would be best resolved by further detailed study of simple forms, such as *O. Bergianum*. Here as in *Botrychium* the slit, though apparently transverse, is actually distal and therefore "longicidal" in Von Goebel's terminology.

The structure of the sporangium of *Ophioglossum* as it approaches the stage of separation of the spore-mother-cells is shown in Figs. 328, 329. The sporangial wall is massive, and the tapetum is variable, consisting of ill-defined tabular cells, which lose their identity and fuse into a continuous plasmodium.

¹ See K. and L., pl. ix., Fig. 58, or Scott's *Studies*, Fig. 177.

² Von Goebel, *l.c.*, p. 1290, Fig. 1376.

Their nuclei persist and increase in number, apparently by fragmentation. Presently the plasmodium penetrates between the sporogenous cells, the whole mass being gradually broken up into irregular blocks (Fig. 329, *A*), and later the individual cells separate (Fig. 329, *B*). Normally all these spore-mother-cells undergo tetrad division, and form spores.¹ But occasional cells are disorganised, as may happen in many large sporangia. It may be that the degree of such disorganisation depends upon the available nutrition. In any case there is the analogy of *Equisetum* and of *Psilotum* to support such a view (Fig. 93).

The peculiar sporangiophores borne on the spike of *Helminthostachys* have been discussed in Chapter XVIII. The facts do not suffice to give an interpretation of them in exact terms of dichopodial origin. Whatever be the ultimate opinion on these unique structures, the sporangia which they bear are of the same type as those of *Botrychium*. There is no mechanical annulus in any of the Ophioglossaceae, but the slit of dehiscence is defined structurally before the sporangium opens.

The sori of the Marattiaceae have already been described (p. 366, Fig. 302); and again two types appear, viz., those with the constituent sporangia separate as in *Angiopteris* (*A*, *B*), and those with fused synangia as in *Marattia* (*C*, *D*, *E*). These may be compared respectively with *Botrychium* and *Ophioglossum*. There is no standardised indusium, though hairs may be associated with the sori, and in *Danaea* upgrowths from the leaf-surface partly shield them. These sori are all constructed on the radiate plan, with a single series of simultaneous sporangia facing inwards to a central point or line. The structure of the massive sporangia is essentially uniform, whether they are separate or fused into synangia. That the synangial type is an ancient one is shown by the existence of the Carboniferous fossil *Ptycho-carpus* (Fig. 301). The development and mature structure as seen in the separate sporangia of *Angiopteris* will serve as an example of them all, subject to some differences of detail.

At an early stage the massive sporangia of *Angiopteris* begin to project as separate outgrowths from the soral area, which lies immediately over a vein (Fig. 330, *A*). Of those shown, that marked (*b*) is the most regular and usual type, and a single superficial cell, centrally placed and here already

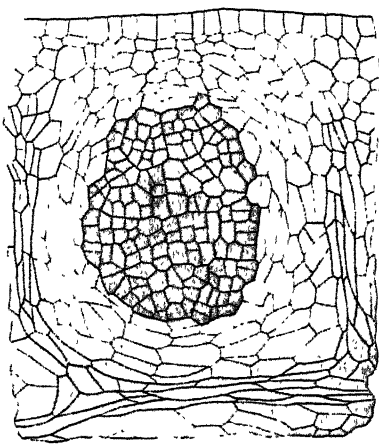


FIG. 328.

Ophioglossum reticulatum, L. Longitudinal section through a sporangium before separation of the spore-mother-cells; the walls of the vascular tissue are drawn in rather more heavily. $\times 100$.

¹ Burlinghame, *Bot. Gaz.*, 1907, p. 34.

divided into two, gives rise to the essential part of the sporangium. If a median section were taken through such a sporangium, but slightly more advanced, it would appear as in (*B*), the cells shaded corresponding to those shaded in (*A*). Periclinal division separates the sporogenous tissue from the protective wall (*B*, *C*). As development proceeds the divisions are sufficiently regular to indicate the genetic grouping of the tissues. The sporogenous tissue is early defined by the dense protoplasm of its cells, and they

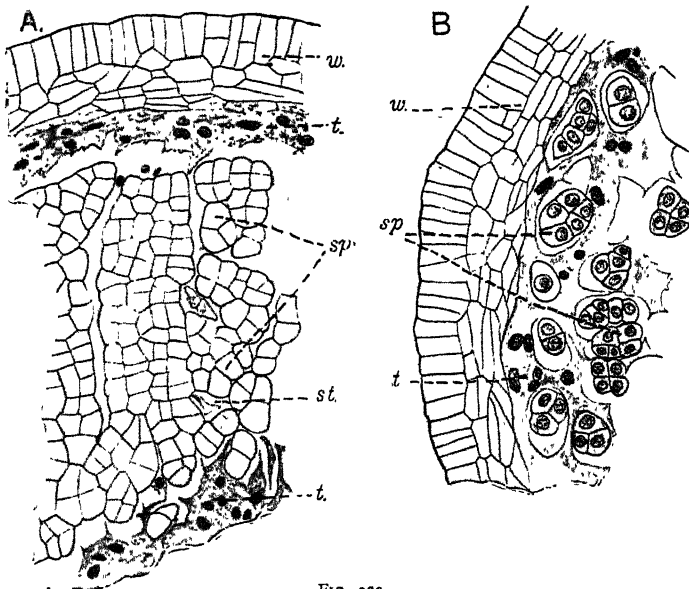


FIG. 329.

Ophioglossum vulgatum, L. Portions of sporangia showing the sporogenous tissue in two stages of disintegration. In *A* the tapetum (*t*), evidently derived from more than a single layer of cells, has formed a plasmodium with many nuclei, which is beginning to penetrate the sporogenous tissue, in which an occasional cell (*st*) is seen disorganised. *B* shows a more advanced state, where the sporogenous cells (*sp*) appear in small clusters, or isolated, embedded in the tapetal plasmodium (*t*); *w*=sporangial wall. $\times 100$.

are clearly referable to a single parent-cell. The cells immediately surrounding the sporogenous group assume the character of a tapetum (*E*). Meanwhile certain cells at the apex of the sporangium enlarge to form the crest-like ridge of the annulus, which is present here as it is in *Zygopteris* (Fig. 272). From this downwards on the central side of the sporangium the dehiscence will take place. Fig. 330, *E*, represents a sporangium which has arrived at the stage of complete division of the sporogenous group, and the spore-mother-cells are about to round themselves off prior to tetrad-division. The spore-output of each sporangium may be computed by estimating the number of spore-mother-cells, as revealed by transverse and longitudinal sections; the result is about 360, giving about 1440 spores if all the mother-cells are fertile.

Outside the sporogenous cells and tapetum lies the sporangial wall, consisting usually of three layers, of which the outermost cells are the firmest: part of it gives rise to the opening mechanism. The cells shaded in (*F*) are large, turgid, and thin-walled: the lateral bands enclosed by brackets consist

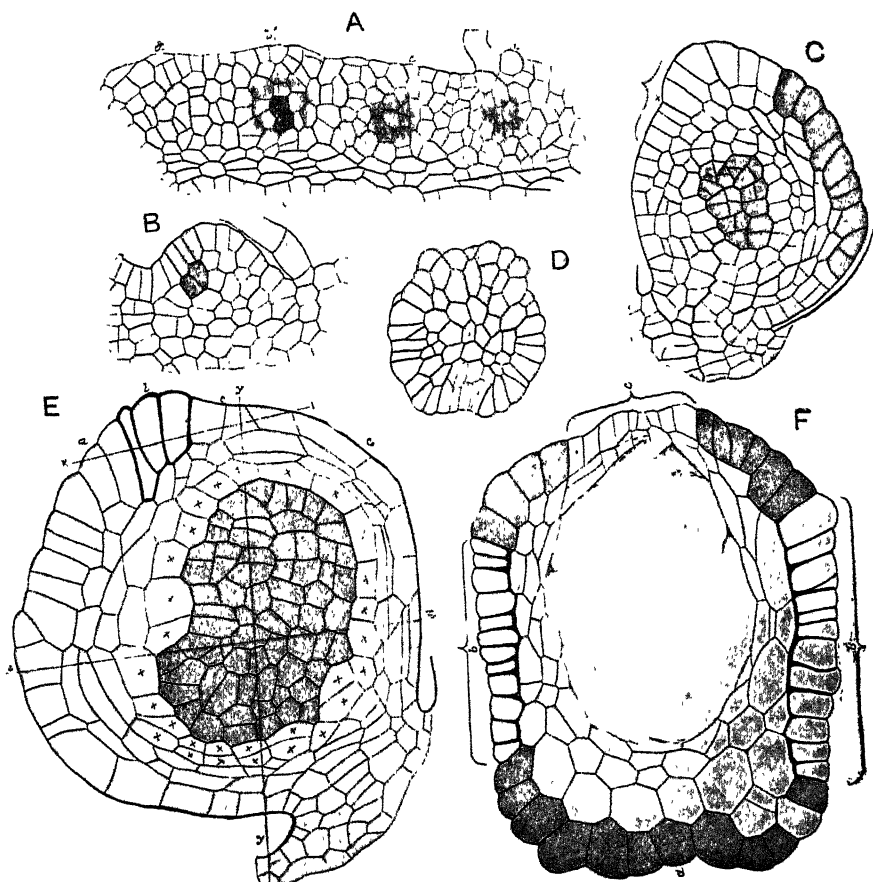


FIG. 330.

Angiopteris evecta, Hoffm. A = part of a young sorus seen in surface view from without. B = vertical (radial) section of a sporangium such as would be seen on cutting the sporangium (b) in Fig. A along the line indicated. C = vertical section of an older sporangium, showing genetic grouping of cells. D = apex of an almost mature sporangium seen from above; such a section as along the line x, x, in Fig. E. E = vertical section of a sporangium with spore-mother-cells; the tapetum is marked x. F = transverse section of an almost mature sporangium. All $\times 200$.

of prismatic cells with lignified walls, which form a mechanical ring continuous across the apex of the sporangium; it is seen in surface view in (*D*). On the ventral face the cells are smaller and thin-walled: they define the line of longicidal dehiscence, which is followed by the plane of section of (*E*). When ripe the shaded cells shrink; the sides of the indurated hoop are thus

drawn together, while the apical crest or ridge, like a semi-rigid hinge, yields so that the slit gapes widely, as it is seen to do in ripe sporangia.

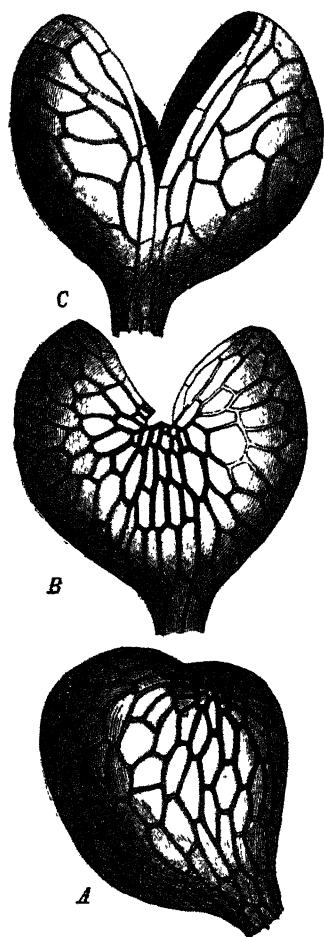


FIG. 331.

Toodea barbara, Moore. Sporangium. *A*, in side view, closed. *B*, seen from behind. *C* from in front, in both cases after dehiscence; the annulus is darkly shaded. $\times 80$. (After Luerssen.)

In the synangial genera the type of sporangium is the same, but without the mechanical arch, the successful working of which would depend on the freedom of the sporangia to change their form. In these genera the shrinkage of the cells adjoining the slit or pore enlarges the opening, while in *Marattia* a hinge-mechanism serves to separate the two halves of the synangium which face one another till ripeness. Comparing such facts with those in the fossils, there is no mechanical arch in the synangial *Ptychocarpus*, but in *Eta-pteris* a similar type to that in *Angiopteris* is present, and would be effective in its free sporangia (Fig. 295). Also, in *Corynepteris* a massive annulus is found (Fig. 296); from which it may be concluded that the sporangia composing the compact sorus were not united into a synangium. As regards spore-output the estimated numbers in the synangial types are higher than in *Angiopteris*: for instance, *Danaea* 1750, *Marattia* 2500, and in *Christensenia* over 7000. This accords with like estimates for the Ophioglossaceae, where the synangial sporangium is also the more prolific. But, on the other hand, Halle's spore-counts for the Rhaetic fossil *Danaeopsis fecunda* were only 1100 to 1159.¹ Such figures cannot naturally be expected to tally exactly: nevertheless those quoted point to some biological advantage following on the synangial state over that of isolated sporangia. For the Marattiaceae

at large the spore-output from each sporangium is over 1000: such a figure appears to be the usual minimum for Eusporangiate Ferns.²

Leaving now the typically Eusporangiate Ferns we pass to the Osmundaceae, which have been seen to take a middle position between the Eusporangiate and Leptosporangiate Ferns in respect of the vegetative structure of

¹ *Arkiv. für Botanik*, Bd. xvii., 1921.

² *Ferns*, vol. ii., chap xx.

the sporophyte. Comparison of the structure and development of their sporangia shows that in these also they supply a connecting link. The adult sporangium is pear-shaped, and relatively thick-stalked. It consists at maturity of a single layer of cells forming the wall, but with a few tabular cells lining it within. A group of polygonal thick-walled cells in a lateral position near to the distal end is recognised as the annulus : it is related to the slit of longitudinal dehiscence so that the latter passes from the centre of the group, over the distal end, and approaches the stalk on the opposite side of

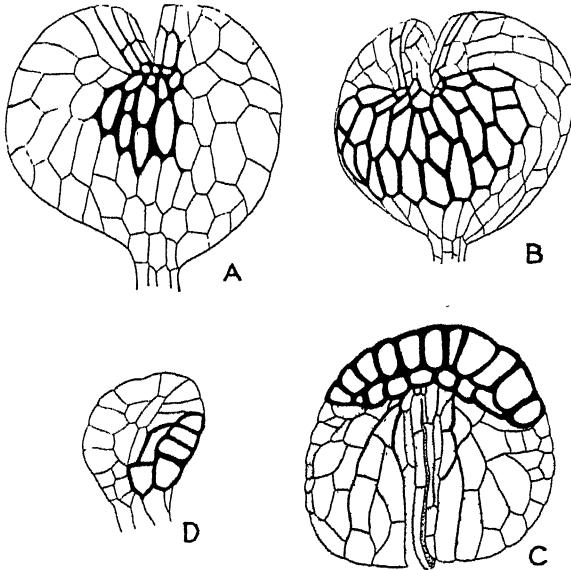


FIG. 332.

Sporangia of *Todea barbara*. A, B, normal types with differences of mechanical tissue. C, normal sporangium seen from above, with detail of dehiscence. D, an abortive sporangium. $\times 120$. (After Williams.)

the sporangium (Figs. 331, 332). The line of dehiscence, defined structurally by narrow thin-walled cells, gapes widely at ripeness : this requires elbow-room, which the lax grouping of the sporangia readily allows. The origin of the sporangia is simultaneous.

The development of the sporangia in the Osmundaceae differs from that of most Ferns in the variety of its details in individual sporangia, even when they may be close neighbours on the same pinnule. The sporangia vary considerably in size, and in structure ; even the opening mechanism is subject to differences of wide range (Fig. 332). In development they are found to fluctuate between two types of segmentation, which are shown in Fig. 333. Here are detailed drawings of two sporangia of *Todea barbara*, one with a square-based archesporial cell as in Eusporangiate Ferns, the other with the conical type characteristic of the Leptosporangiates : the latter is the

commoner in the Osmundaceae. The differences start from the first cleavages, as appears from Fig. 334, *A*, where two sporangia side by side differ; this drawing also shows that the cells marked (*x*) do not compose the whole out-

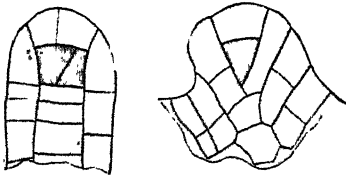


FIG. 333.

Young sporangia of *Todea barbara* in longitudinal section, showing different modes of segmentation. $\times 365$.

growth: adjoining cells also contribute, so that strictly speaking this type is not Leptosporangiate. How various the subsequent cleavages may be is suggested by the drawings *A* to *E*. Differences in bulk appear in sporangia of the same age (*C*, *D*), and sections through the stalks bear this out in a later stage, as in the two drawings at the centre of the group of

Fig. 334. The superficial cell at the centre of the outgrowing sporangium usually divides by three anticlinal walls corresponding to those seen in the ordinary Leptosporangiate type, though the cell which remains in the middle may still be either truncate or pointed at the base (Fig. 334, *A-D*). Then

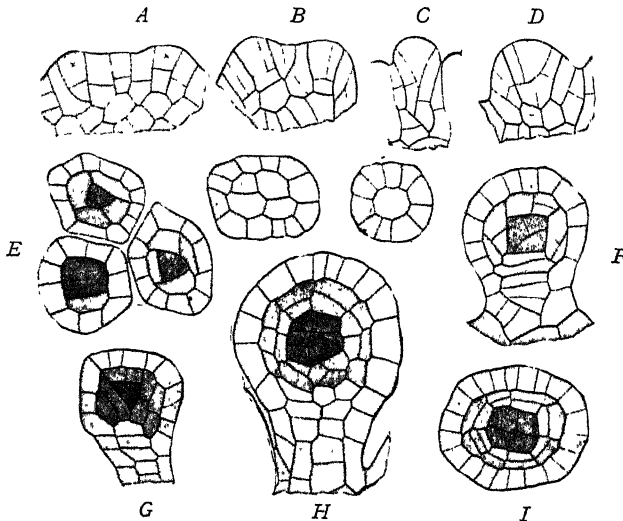


FIG. 334.

Todea barbara, Moore. *A*=small part of section of pinnule showing two young sporangia (*x*, *x*). *B*, *C*, *D*=examples of variety of segmentation, as seen in vertical sections. *E*=older sporangia in transverse section, showing differences in sporangia in juxtaposition. *F*=vertical section of sporangium of like age, with square-based sporogenous cell. *G*=similar sporangium with triangular sporogenous cell. *H*, *I*=vertical and transverse sections of older sporangia. The central figures show two unequal sporangial stalks, in transverse section. All $\times 200$.

follows the periclinal division to separate the cap-cell. The archesporial cell, thus surrounded by tissue which will form the sporangial wall, undergoes further divisions to form the tapetum (*E-G*), while the sporogenous cell subdivides to form the spore-mother-cells. The origin and early structure of the

sporangium in the Osmundaceae is thus seen to be more robust than in the ordinary Leptosporangiate Ferns. This leads to the later stage seen in Fig. 335, which shows a relatively large number of sporogenous cells, a tapetum consisting partly of three layers, and the stalk, with a central core surrounded by a superficial layer. In all of these points the Osmundaceous sporangium is more complex than the ordinary Leptosporangiate type.

In *Osmunda* Russow long ago estimated the number of spores in a single sporangium as over 500, and assumed therefore the number of spore-mother-cells to be 128.¹ An estimate based upon sections before the tetrad-division confirms this figure approximately, while actual countings show for *Osmunda regalis* figures fluctuating between 256 and 512. In *Todea barbara* the numbers are often nearer to 256, while in *T. superba* and *hymenophylloides*, which are "filmy" in habit, the output may be still lower, even approximating to 128 in the latter species. These results readily accord with the relatively robust but variable structure of these sporangia, as compared with those of ordinary Leptosporangiate Ferns, where the number of spores is only 64, or often less. In the Male Shield Fern it is 48. Thus the sporangia of the Osmundaceae take a middle position between the massive type of the Eusporangiate Ferns and the more delicate Leptosporangiates, not only in their development and structure but also in their spore-output.

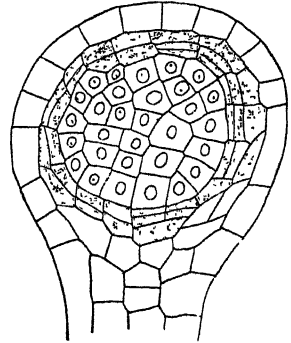


FIG. 335.
Sporangium of *Osmunda regalis*, containing a large sporogenous tissue, surrounded by tapetum consisting in parts of three layers. (After Goebel.)

In the primitive Ferns the sporangia appear to be less standardised than in those that are more advanced. For instance, the sporangia of the Male Shield Fern are usually all alike, and of approximately uniform size; they have a three-rowed stalk, and an annulus composed of a single row of cells of definite number. But among the Eusporangiate Ferns and the Osmundaceae the size and structure of the adult sporangia may vary within wide limits, even in those in close proximity on the same plant. It has already been seen how the young sporangia of *Botrychium* may vary in breadth, and that even fission may appear (Fig. 298). Such instability of the individual becomes a more marked feature in the synangial spikes of *Ophioglossum*, and striking examples of it are seen in *Danaea*. Here the single sorus may extend the whole distance from the margin of the blade to the midrib (Fig. 302, E). This suggests an extension of a synangium of the type seen in *Marattia* (C): the structure of the sorus and of its constituent sporangia supports such a view. If a tangential section be cut the appearance may be as in Fig. 336. Each of the elongated sori appears as a double row of fused sporangia; but the interesting point is that they are very variable in size and in their relation one to another.

¹ *Vergl. Unters.*, 1872, p. 87.

Frequently they appear in pairs, with a thin or even an imperfect septum dividing them; occasionally three may be so related (*A*). The septum while young may be partly composed of permanent tissue, partly of tapetum which would break down to the usual plasmodium as maturity comes on (*B*). Such facts show a high degree of instability of the sporangium as a unit: they suggest that this follows on elongation of the synangium, leading to an increase in the number of its component sporangia by fission.

A similar instability is seen also in the Osmundaceae. Occasionally it appears in the form of a double sporangium, each unit showing a structure like that of a normal unit (Fig. 337). This may be compared with the state already

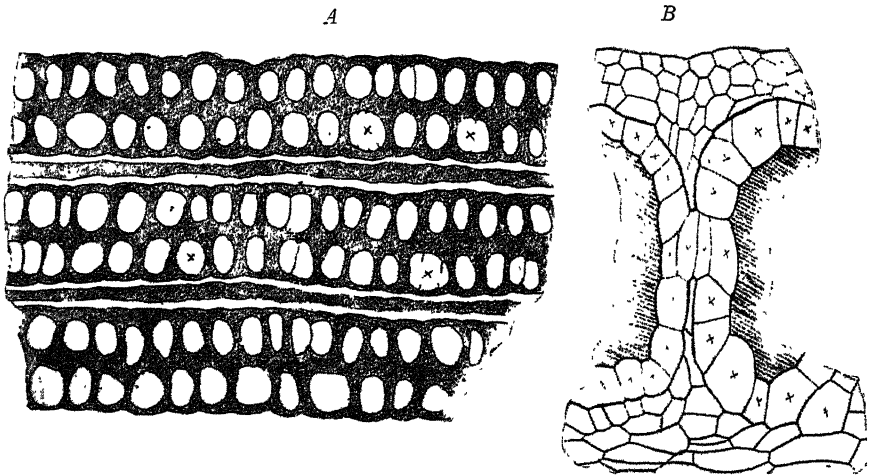


FIG. 336.

Danaea elliptica, Smith. Drawings illustrating partial septations of the sporangium. *A*, tangential section through three sori, showing the loculi in ground plan: the septa are often thin, so that pairs of loculi are in close juxtaposition; the loculi marked (x) are large, and show one or more partial septa. $\times 20$. *B* shows two loculi with a partial septum in greater detail; here the tapetal cells are marked (x). $\times 150$.

noted for *Botrychium* (Fig. 298), both being suggestive of a primitive branching. More commonly it appears as a difference in size, as has been already seen in the young stages of *Todea* (Fig. 334, *C*, *D*). It also appears in the adult state (Fig. 332, *A*-*C*), and particularly in sporangia borne about the limit between the sterile and fertile tracts, where the size may be minute (*D*). Differences in the structure of the annulus are also a marked feature: the indurated cells may form only a small group (Fig. 332, *A*); or more frequently the annulus appears as a band 8-11 cells broad and 2-3 rows deep (*B*), a state comparable with that of *Kidstonia* from the Coal Measures (Fig. 342, *B*). From such observations it appears that the sporangia of the Eusporangiate Ferns, and of types referred to the Osmundaceae, are more variable in size and structure than those of the more standardised Leptosporangiate Ferns. Nevertheless somewhat similar irregularities in the constitution of the stalk, and of the mechanical cells, are found in some of the relatively primitive Leptosporangiate types. These suggest a special instability in those genera in which the single-rowed annulus has not become a fully settled feature. Particularly interesting

irregularities were described by Kny for *Ceratopteris* (*Parkeriaceae*, Dresden, 1875). J. McL. Thompson has reported similar abnormal development in *Platyzoma*.¹ In *Cryptogramme* again these are combined with variations of structure of the stalk. Slighter departures from the normal are also recorded for *Plagiogyria*.² The interest of these deviations lies in the fact that all the Ferns named are relatively primitive among the Leptosporangiates. It seems legitimate to suggest that in them the sporangium has not been structurally standardised, so far as to give to the annulus or to the stalk the stable character seen in the more advanced types. This generalisation, however, does not cover all cases: for instance, marked examples of an abnormal annulus have been recorded in *Acrostichum aureum*, a highly specialised Pteroid Fern.³

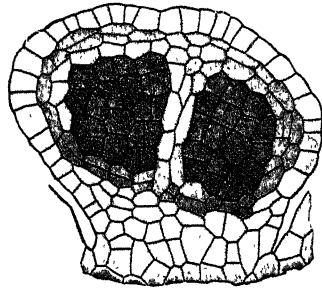


FIG. 337.

Osmunda regalis. A synangium, in vertical section. $\times 200$.

The Schizaeaceae offer in the details of their sporangia another significant bridge to those of more specialised Ferns; similarly, this family has already been seen to supply a like transition in the form and structure of the vegetative system. The persistent marginal origin of the sporangia, tending

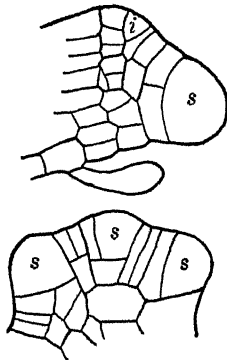


FIG. 338.

Mohria caffrorum, drawings after Prantl, showing the relation of the sporangia (s) to the marginal series, and to the indusium (i), as seen in surface view, and in section. $\times 145$.

later towards the lower surface, was observed by Prantl (Fig. 338). The result in the adult state has been shown in Fig. 304, with which Fig. 293 may also be compared. The sporangia thus produced, and variously protected by indusial flaps, closely resemble those of *Osmunda* and *Todea* (Fig. 330). In particular a comparison of the adult sporangium of *Mohria* (*D*, *E*) with that of *Todea barbara* (Fig. 332) shows little difference; allowance being made for the variability now recognised in *Todea*. The individual sporangia are large and sessile, or in *Lygodium* shortly stalked, and they are annulate, and oval or pear-shaped. The annulus in the living genera is usually uniseriate, though occasionally it is more complex: it is distal, and there is a definite stomium with longicidal dehiscence. However

contracted the annulus may appear there is in its centre an apical group of cells styled by Prantl the "plate," which may better be called the "distal face" of the sporangium: it is an important feature for comparison with more specialised Ferns. Sometimes it consists of only one cell (*Lygodium*,

¹ *Trans. R.S. Edin.*, li, lii, 1916, 1917.

² For further details see *Ferns*, iii, chap. xxxix.

³ Schumann, *Flora*, 108, 1915, p. 220.

Fig. 339, *C*; *Schizaea*, *A*, *B*); sometimes of many (*Anemia*, *F*, *G*, or *Mohria*, *D*). Usually its cells are thin-walled, but in *Mohria* they are thick-walled and irregular (*D*). The rest of the sporangial wall is thin. In *Mohria* the sporangia are radially constructed, as in the Osmundaceae, apex and base

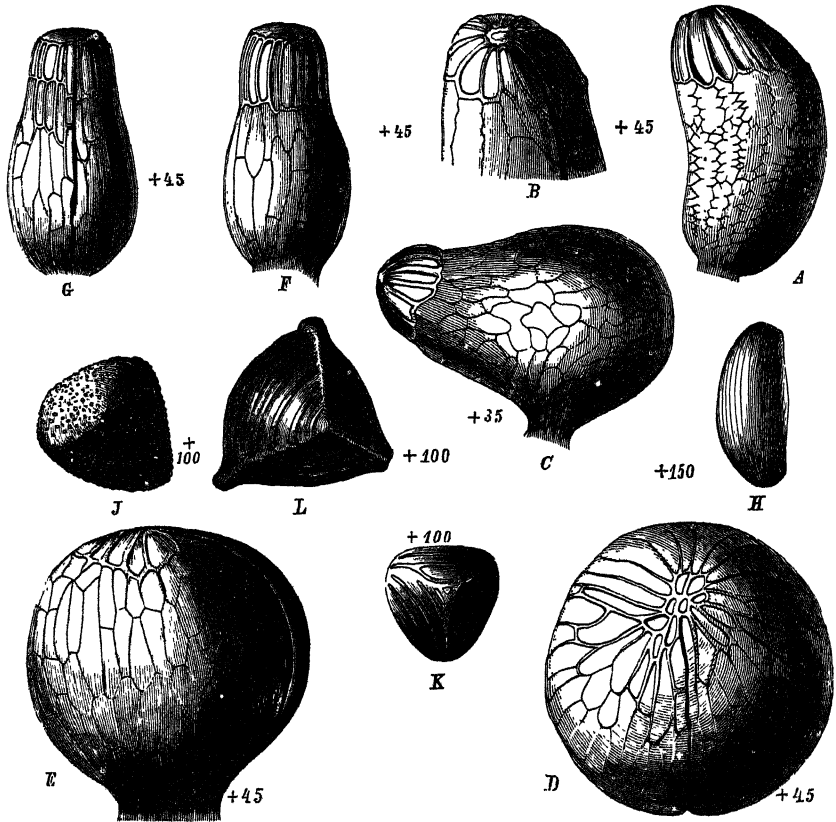


FIG. 339.

Sporangia of the Schizaeaceae. *A*, *B*=*Schizaea pennula*, Sw. *A* seen laterally. *B*, the tip seen obliquely from above. *C*=*Lygodium japonicum*, Sw., seen laterally. *D*, *E*=*Mohria caffrorum* (L.) Desv. *D*=seen from above. *E*, laterally. *F*, *G*=*Anemia Phyllitidis*, Sw. *F*=view from midrib, *G* from margin of pinnule. *H*-*L*=spores of the Schizaeaceae. *H*=*Schizaea pennula*, Sw. *J*=*Lygodium japonicum*, Sw. *K*=*Mohria caffrorum* (L.) Desv. *L*=*Anemia fulva*, Sw. (All but *K* after Prantl. *K*, after Diels—from Engler and Prantl, *Nat. Pflanzenfam.*)

being opposite (*D*, *E*); but in other genera the body of the sporangium is more or less curved, especially in *Lygodium* (*C*).

Certain fossils which have been referred to this affinity help towards an understanding of the living forms. *Senftenbergia* from the Upper Carboniferous was described by Corda as of Schizaeaceous character, with a Pecopterid leaf bearing sporangia as in *Anemia* (Fig. 340). More recently P. Bertrand has described as *Pecopteris pennaeformis* Brongn. a fossil from the Coal Basin

of Northern France of similar character. He finds the isolated sporangia orientated as in *Anemia*, but larger, with an indurated annulus consisting of two or three rows of cells, with a definite stomium, but with no "plate" or distal face. These features do not differentiate these fossils from all living Schizaeaceae, for in *Mohria* there is no thin-walled plate, while various species of *Lygodium*, a genus which itself dates from Cretaceous times, have a partially double series of cells of the annulus (Fig. 339, *G*). Whether or not these fossils be rightly referred to the Schizaeaceae there can be little doubt of *Klukia*, a Jurassic fossil, with an arrangement of the sporangia as in *Schizaea*, which it also resembles in its single series of cells of the annulus,

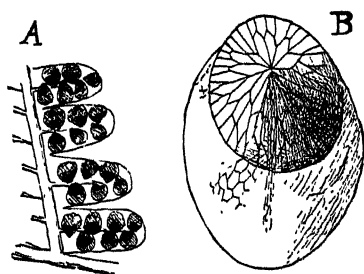


FIG. 340.

Senftenbergia (Pecopteris) *elegans*, Corda.
A = a small piece of sporophyll (♂). B = a sporangium (♀). (After Zeiller, from Engler and Prantl, *Nat. Pflanzenfam.*)

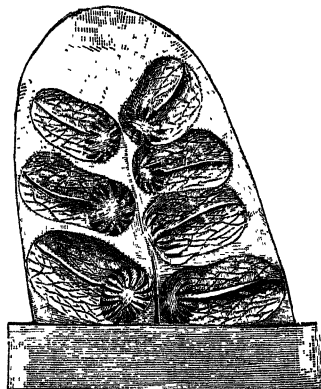


FIG. 341.

Klukia exilis (Philippe), Raciborski.
Fertile pinnule of last order, seen from below (♀). From the Jurassic of Krakau. (After Raciborski, from Engler and Prantl, *Nat. Pflanzenfam.*)

and in the line of longicidal dehiscence (Fig. 341, 342, *C*). From such comparisons it appears that the Schizaeaceous type is an ancient one, and, in particular, that the sporangia had originally a more complex annulus than is usual at the present day. In this connection the fossil *Kidstonia* (Fig. 342, *B*) has a special interest, though its systematic position is still indeterminate; its existence strengthens the comparisons of the Schizaeaceae with the Osmundaceae, and ultimately perhaps with some Zygopterid type.

The similarity of the adult sporangia of the Schizaeaceae to those of the Osmundaceae will focus special interest on the details of their development. Prantl had already in 1881 noted that, in them all, the first segment-wall of the young sporangium extends from the outer to the inner periclinal walls of the roughly cubical primordial cell. This is characteristic of a more robust sporangium than that of the advanced Leptosporangiates; but it corresponds to the simpler of the two types seen in *Todea* (Fig. 343, also 333, 334). Here the whole outgrowth of the sporangium is not referable to a single parent cell, thus showing clearly a transition from the Eusporangiate state. A like

segmentation is seen also in *Thyrsopteris* and *Trichomanes*. Otherwise, and particularly in the three last lateral segments, the primary cleavages in the Schizaeaceae are of the usual Leptosporangiate type. Then follows the

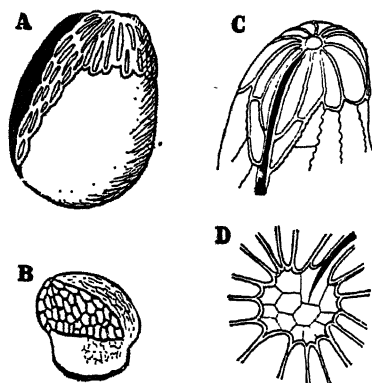


FIG. 342.

A=a sporangium of *Lygodium lanceolatum*. $\times 50$. Showing an annulus of more than a single row of cells. B=*Kidstonia heracleensis*, Zeiller, seen laterally. $\times 50$. C=*Schizaea*, apex of sporangium with distal wall of a single cell ("Platte"). D=that of *Anemia* with many cells.

periclinal cleavage to form the cap-cell. The subdivision of the archesporium thus enclosed results in the tapetum and sporogenous group. The latter consists, however, of a larger number of spore-mother-cells than is commonly seen in Leptosporangiate Ferns; while the tapetum may consist of more than the usual two layers (Fig. 344). Spore-countings for *Lygodium japonicum* give about 256 per sporangium; but in *L. pinnatifidum* only about 128, and this lower figure is shared by *Schizaea*, *Mohria* and *Anemia*. Thus, whether in early segmentation or in spore-output, the sporangia of the Schizaeaceae, and particularly of certain species of *Lygodium*, compare with

the Osmundaceae and other palaeozoic types, and link these with the modern Leptosporangiates, where the number is 64 or less. These comparisons have been given in detail in order to show how intimate may be the features which form the bridge between the Palaeozoic and the later types of Ferns.

The Gleicheniaceae, with their superficial, rosette-like sori, present again an archaic sporangial type, quite in keeping with the early occurrence of their congener *Oligocarpia* from the Coal Measures (Fig. 345, A, B). The living genus includes species characterised by having respectively sporangia of two rather distinct types: a larger type of which 4 to 6, or less, are grouped in each sorus, represented by *G. flabellata* or *circinata*; and a smaller type of which 6 to 12 may be borne on each sorus, as in *Gleichenia* (*Dicranopteris*) *linearis* and *pectinata* (Fig. 345 bis). The former are globose, with a relatively short stalk (*i, j, k*); the latter pear-shaped, with a thinner and longer stalk (*l, m, n*). In both there is a complete oblique annulus, and median (longicidal) dehiscence. The sporangial wall is clearly marked off by the ring into two thin-walled regions, the proximal or basal lying between the annulus and the stalk, and the distal face or "plate" of Prantl; the latter is here convex, and consists of a large number of cells. The spore-output



FIG. 343.

Diagram of segmentation of a sporangium of the Schizaeaceae; the first segment wall meets the periclinal (basal) wall of the parent cell; but the second (*x, x*) meets the first, and does not extend to the base of the parent cell.

for *Gl. flabellata* lies between 512 and 1024: in *Gl. linearis* it is often considerably below 256. The sorus arises as a smooth superficial outgrowth opposite to a vein (Fig. 346, *a*), and the sporangia appear as rounded processes upon it. There is some divergence of detail in their segmentation according to the size of the future sporangium. In the larger type (*b*) there appears less exact sequence than in the smaller (*g*), and this accords with the difference of the adult structure of the stalks (Fig. 353 *bis*, *a*, *b*). The form of the archesporial cell is also less definite in the larger type than in the smaller; but its further segmentation follows the ordinary rule, resulting in a double tapetum, and a mass of spore-mother-cells. The number of these as seen in section fully bears out the difference in number of the spores matured by either type (Fig. 347).

The species upon which these data are based are extreme types for the

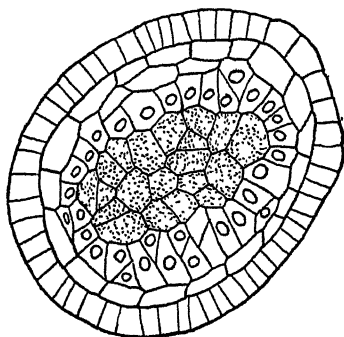


FIG. 344.

Section through a sporangium of *Lygodium circinnatum*; 20 spore-mother-cells are cut through, and the tapetum is of more than two layers. (After Binford.) $\times 480$.

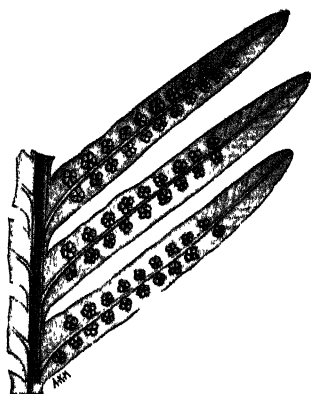


FIG. 345A.

Gleichenia flabellata, Br. Midrib and three pinnules, showing the arrangement and constitution of the sori, with variable number of sporangia.

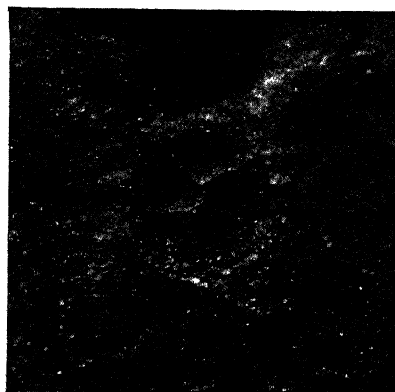


FIG. 345B.

Sorus of *Oligocarpia Gutbieri*, Göppert, from a photograph by the late Dr. Kidston. The annulus had the appearance of being a single series of cells. It was difficult on examination of the specimen to be sure there was no synangial fusion, but the presence of the annulus would make fusion appear to be improbable, as the annulus would then be functionless.

genus, both in respect of size of the sporangia and in their individual spore-output. Comparison of what is seen in them with the corresponding facts in the Osmundaceae and Schizaeaceae shows that the Gleicheniaceae are not

behind these families in the absence of any exact standardisation of their sporangial structure. Such facts suggest a transitional state for all of them, with the smaller sporangia for each family pointing in the direction of those typical for Leptosporangiate Ferns. Whether the sori be marginal or superficial each of these families appears to form a bridge between the Eusporangiate and the Leptosporangiate types of Ferns. Moreover, they all have a history extending back, with high probability, to the Palaeozoic Period.

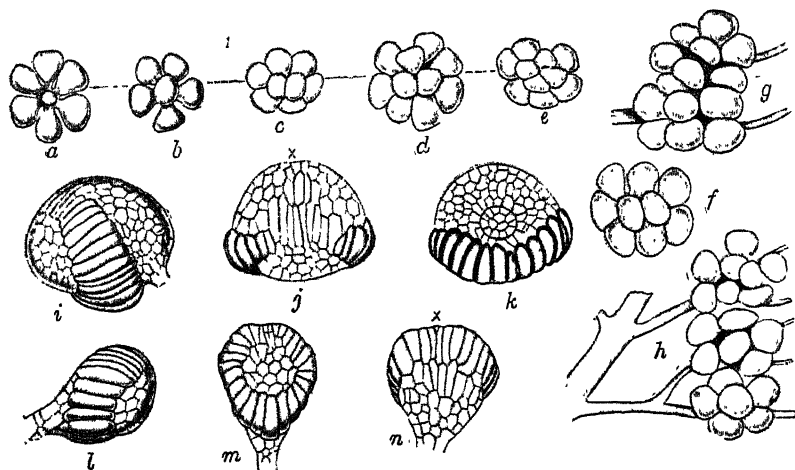


FIG. 345 bis.

a-h=sori of *Gleichenia linearis*, Willd. *a-c* show sori of radiate type, but with one or more sporangia in the centre of the sorus, usually in this genus vacant. *f, g, h* show degrees of fission of the sorus. *a-h* \times about 14. *i, j, k*=sporangia of *Gleichenia circinata*, Sw., seen respectively from the side, from the distal end showing the line of dehiscence (*x*), and from the proximal end showing the stalk. \times 50. *l, m, n*=sporangia of *Gleichenia linearis*, Willd., seen respectively from the side, presenting the distal and proximal faces. Note the difference in size from *G. circinata*. \times 50.

The families described in this Chapter, to which may be added the Matoniaceae, a type traced back to the Jurassic Period, are all *Simplices*, in the sense that their massive sporangia are locally simultaneous in origin, and relatively massive in structure; and they all have a high individual spore-output, excepting *Matonia*. With regard to sporangial development Scott remarks that "it is doubtful if the distinction between Eusporangiate and Leptosporangiate Ferns existed in Palaeozoic times: in other words, "whether the development of the sporangium from a single cell had yet been arrived at."¹ Kidston has also expressed himself in similar terms. Indeed, it may further be doubted whether any annulus consisting of a single row of cells existed in the Primary Rocks. Thus the general conclusion based on a comparative study of living Ferns is substantiated from the Fossil Record. In development and character the Palaeozoic type of sporangium

¹ *Studies*, 3rd ed., p. 366.

in Ferns was relatively massive, with a short and thick stalk : it sprang from the outgrowth of a plurality of cells ; had a longicidal dehiscence operated by mechanical tissue not highly specialised ; and each sporangium produced numerous spores : their number was usually about 1000.

The modern representatives of ancient stocks seen in the living Osmundaceae, Schizaceae, and Gleicheniaceae all point towards a progressive refinement of sporangial structure such as this, particularly in a reduction of

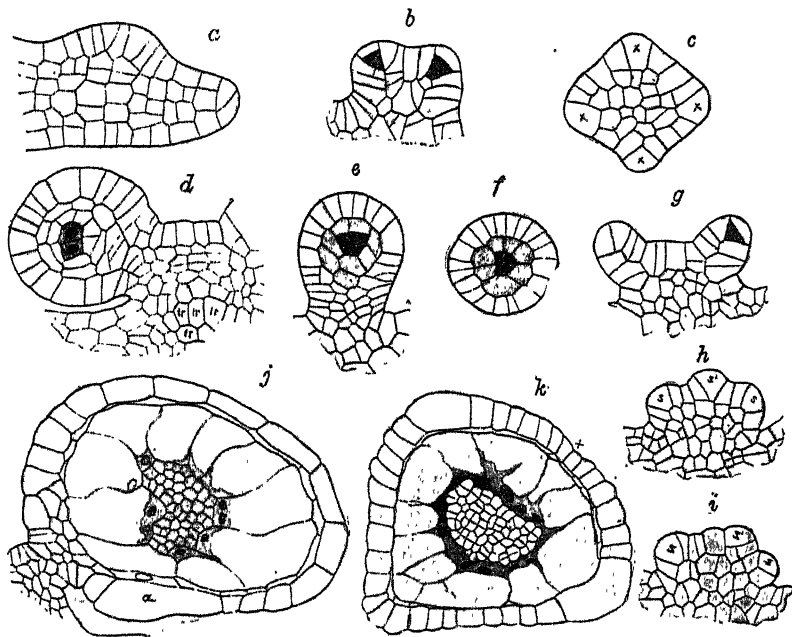


FIG. 346.

a, b, c=sori of *Gleichenia flabellata*, a, b in vertical, c in horizontal section ; d, e, f=sporangia of *Gl. circinata* showing central cell and tapetum ; g, h, i=sori of *Gl. linearis* ; in g the centre is vacant, in h and i young sporangia appear in the vacant space ; j, k=sporangia of *Gl. flabellata* with spore-mother-cells formed, and very numerous. a-i $\times 200$; j, k $\times 100$.

size, perfection of mechanism, and lower individual spore-output. But if the productivity of the plant as a whole is to be maintained there must be an increase in the number of sporangial units to balance the diminution in the size and spore-output. Such addition, however, would raise a mechanical difficulty. For successful dehiscence by means of a mechanical ring, such as appears in those Eusporangiate Ferns which have free sporangia, free space would be required beyond that occupied by the ripe capsule itself ; it may be as lateral elbow-room or as free space overhead. As the sporangia multiply, which they are seen to have done in many advancing evolutionary lines, and particularly in *Gleichenia* (Fig. 345 bis, a-h), soral crowding would be the direct

result, and a condition of mechanical dead-lock may be reached. This is illustrated within the genus *Gleichenia*, which has a type of sorus dating back to palaeozoic times. In the Section *Eu-Gleichenia* the sporangia are short-stalked, globose, and few in number in each sorus (4-6): they are arranged as

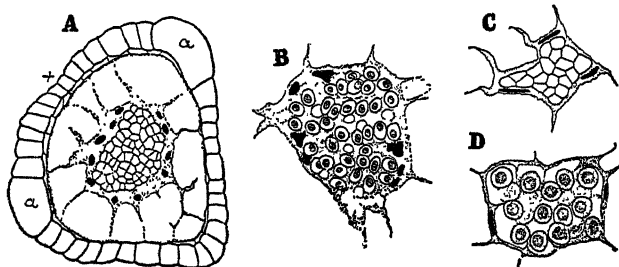


FIG. 347.

A=section of a sporangium of *Gleichenia flabellata*, showing over 60 spore-mother-cells in section. $\times 100$. B=spore-mother-cells of the same, older and separated from one another in the tapetal plasmodium. $\times 165$. C=spore-mother-cells and tapetal plasmodium of *Gleichenia linearis*; only 20 are seen in section. $\times 100$. D=cells of the same separated in the tapetal plasmodium. $\times 165$.

a rule on a radiate-uniseriate plan round a central receptacle, and there is sufficient latitude in the lax group of sporangia for each to open; this is seen, for instance, in *Gl. linearis* (Fig. 348). But in the Section *Dicranopteris* the number may be larger (6-12): even the centre of the ring may be occupied

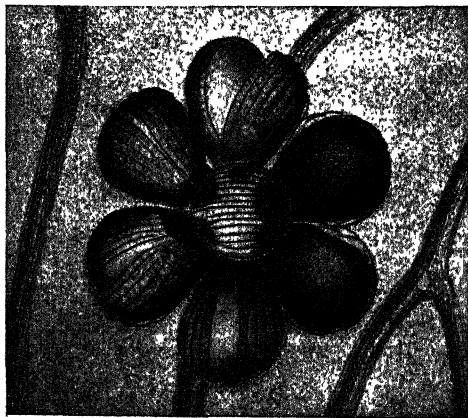


FIG. 348.

A single sorus of *Gleichenia linearis* showing lax disposition of the sporangia, several of which have opened by a median slit. Enlarged. (Drawn by Mr Maxwell.)

by a group of sporangia, which are so closely packed that their contiguous sides are flattened, as in *Gl. pectinata* (Fig. 349). There is not sufficient elbow-room for all to dilate on opening, and it is often found that sporangia after full ripeness still retain their spores. A simple elongation, or a widening of the receptacle, would meet the consequent dead-lock; but in *Gleichenia*

neither of these remedies has been adopted. In *Gl. pectinata* that type of sorus has reached its practicable limit. There is, however, still another resource, but again neither *Gleichenia* nor any other of the living Simplices has adopted it: viz., to develop the sporangia of one sorus not simultaneously but in succession. This would bring not only mechanical but also physiological relief. Such changes would co-operate with the progressive

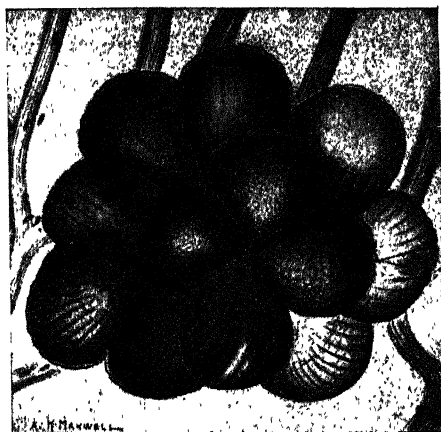


FIG. 349.

A single sorus of *Gleichenia pectinata*. Its sporangia are so closely packed as to be flattened against one another; one has already ruptured; one on the right is inverted. Enlarged. (Drawn by Mr. Maxwell.)

reduction in size and complexity of the sporangial unit, while the mechanism of the ejection of the less numerous spores of each may itself be brought to a higher state of perfection. The steps of specialisation thus briefly sketched may be followed along a plurality of evolutionary lines in living Ferns, leading in divers ways to the soral and sporangial adjustments characteristic of the Leptosporangiate Ferns. They will be described in the next Chapter. The innovations to be expected would then be: (i) elongation of the receptacle, or its spread over a larger area; (ii) a succession of sporangia spread over a prolonged period; (iii) such modifications of the sporangia themselves as add to the efficiency of either of these: for instance, elongation of their stalks, restriction of the spore-output from each, and a highly specialised means of mechanical ejection of the spores.

CHAPTER XX

THE SPORANGIUM OF THE FILICALES

B. THE LEPTOSPORANGIATE TYPE¹

A DESCRIPTION of a normal type of sporangium for Leptosporangiate Ferns, together with the leading facts of its development, finds a place in any elementary course in Botany.² Commonly the sporangium of the Male Shield Fern is chosen as an example. The three lateral cleavages of the sporangial mother-cell, followed by the periclinal cleavage which defines the tetrahedral archesporium, the three-rowed stalk, the laterally compressed capsule with its marginal annulus and transverse dehiscence, the 12 to 16 spore-mother-cells, and the 48 to 64 spores are all features of an ordinary Leptosporangiate type. An attempt must now be made to fit sporangia of such a type comparatively into their natural place in the general progression from the primitive Eusporangiate Ferns to those that are more specialised. The details upon which such comparison is based will be considered under the headings of (1) Initial Cleavages ; (2) the Sporangial Stalk ; (3) the Sporangial Head or Capsule ; and (4) the Spore-Output. These features have been described for certain primitive families or genera of Ferns in the preceding chapter : they will now be examined with special reference to the more advanced types, in which the details cannot be rightly understood until they are compared with those which preceded them.

INITIAL CLEAVAGES

The differences of initial cleavage of the sporangia of various Ferns are suggested by the diagrams in Fig. 350. They pass by gradual steps of attenuation between two extremes shown respectively by (g) and (a) : the

¹ *Selected Literature for Chapter XX* : Kny, *Parkeiaceen*, Dresden, 1875, Taf. xxv. Kny, *Wandtafeln mit erläuterndem Text. Lieferung*, ix., Berlin 1886. Von Goebel, *Vergl. Entwicklungsgeschichte*. Schenk's *Handbuch*, iii., 1884. Bower, "Meristems of Ferns as a Phylogenetic Study," *Ann. of Bot.*, vol. iii., 1889, particularly Plate xxiv. "Studies in Phylogeny of Ferns," i.-vii., *Ann. of Bot.*, 1910-1923. *The Ferns*, vol. i., chap. xiii.; vol. iii., *passim*. Engler and Prantl, *Nat. Pflanzenfam.*, i., 4, with Literature to 1902. Hannig, *Perispore*, *Flora*, vol. 102 (1911), p. 243 ; vol. 103 (1912), p. 321, with full references. Campbell, *Mosses and Ferns*, 1918, *passim*, with full references. Von Goebel, *Organographie*, 1930, pp. 1325-1362. *Ann. Bot. Gart. Buitenzorg*, xxxix., 1928, p. 199.

² Such descriptions will be found in *Botany of the Living Plant*, pp. 472-4 ; or in *The Origin of Land Flora*, pp. 21-23 ; also in *Ferns*, vol. i., chap. xiii.

former is, as we have seen, characteristic of the Eusporangiate, the latter of the Leptosporangiate Ferns. These details of early cleavages, as also many other comparative features of the Ferns in question, show that the distinction between them is only one of degree, not of kind. The palaeontological evidence is decisive in giving precedence in time to the Eusporangiates. In them the sporangium appears as a massive outgrowth which cannot be referred in origin to a single parent cell; nevertheless the fertile tract which produces the spore-mother-cells may as a rule be traced back to a single *cubical cell*—the *Archivesporium*—with relations as indicated in Fig. 350 *g*.¹ The segmenta-

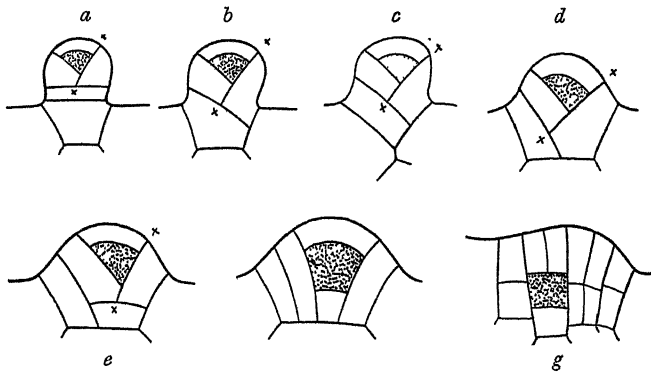


FIG. 350.

Diagrams illustrating the segmentation of Ferns. *a* = Polypodiaceae (compare Kny, Wandtafeln XCIV.). *b* = *Ceraleopteris* (compare Kny, Parkeriaceen Taf. XXV., Fig. 3). *c* = *Alsophila* (compare Fig. 315). *d* = *Schizaea* (compare Prantl, Taf. V., Fig. 69), or *Thyrsopteris*, or *Trichomanes* (compare Prantl, Taf. V., Fig. 92). *e*, *f* = *Todea* (compare Fig. 333). *g* = *Angiopteris* (compare Fig. 330).

tion in the Osmundaceae has already been discussed, and its fluctuation between the types shown in (*e*) and (*f*); the latter bearing a close resemblance to the Eusporangiate type, while the former, with its *Archivesporium* having the form of an *inverted pyramid*, points towards the Leptosporangiate segmentation. It is but a step from this to the type of *Schizaea* (*d*), which is shared by *Trichomanes* and *Thyrsopteris*; but while in (*e*) the wall (*x, x*) is inserted on an inner periclinal, the corresponding wall in (*d*) cuts an anticlinal: this marks a further step in attenuation of the sporangium. The Fig. 350, *b, c* shows the segmentation of various Gradatae: for instance (*c*) corresponds to the condition of *Alsophila* and *Cyathea*, while (*b*) is a slight variant upon it

¹ There has been some uncertainty in the use of the term "*Archivesporium*" as applied to the sporangia of Leptosporangiate Ferns. Von Goebel's own use of it may be seen in his *Organographie*, iii. Aufl., p. 1357. Speaking of the archesporium he says: "Dieser hat meist die Gestalt einer dreiseitigen Pyramide. — Er schneidet bei den Polypodiaceen zunächst vier Tapetenzellen ab: — Darauf wird er in die sporogenen Zellen zerlegt." Thus the term is applied to the central pyramidal cell before the abscission of the tapetum. But in Eusporangiate Ferns the tapetum has its origin from cells surrounding the archesporium—e.g., in *Angiopteris* and *Botrychium*. This shows once more the difficulty of reconciling development with details of cell-lineage.

which is sometimes found, and it is seen in *Ceratopteris*. But in the Polypodiaceae, where the sporangium is commonly long-stalked, the wall (x, x)

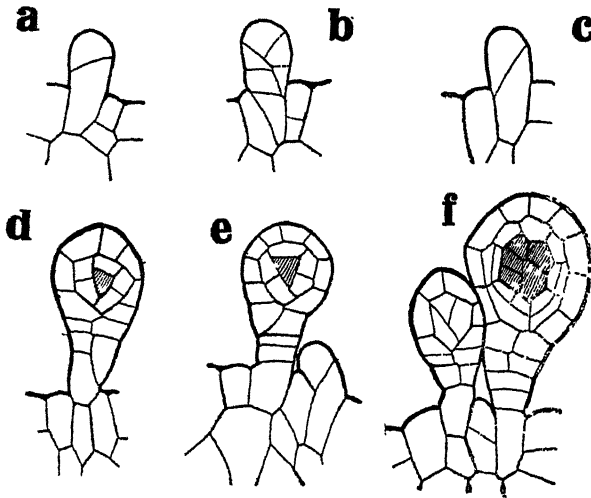


FIG. 351.
Sporangium in *Phlebodium aureum*. *a-f* = stages illustrating the development.
(Compare text.) $\times 200$.

may often be seen to meet a transverse wall (*a*). There may, however, be varying degrees of its obliquity, as is seen in *Phlebodium aureum* (Fig. 351); the first cleavage of the primordium being by an oblique wall (*a, b, c*), which

may extend below the level of the epidermal wall (*b, c*), or be clearly above it (*a*). In the latter case growth of the stalk without further segmentation, as in (*e*), may give the condition of the sporangium seen in *Asplenium* (Fig. 352): here the stalk consists of only a single row of cells throughout the greater part of its length.

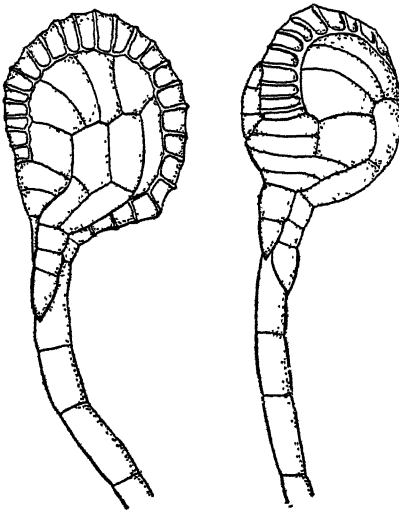


FIG. 352.
Sporangia of *Asplenium Trichomanes*, L. (After C. Muller.)
Showing a stalk of a single row of cells. $\times 140$.

In addition to the two forms of archesporial cell above described, viz., the cubical as seen in the earlier types (Fig. 350, *f, g*), and the tetrahedral, which is described in textbooks as ruling for most of those that are more advanced (*a, c*), there is

also a third type in which the initial cleavages alternate in two rows, and after the formation of the cap-cell the resulting archesporial cell is shaped like half of a bi-convex lens. Examples are seen in *Metaxya*, and *Cheiro-*

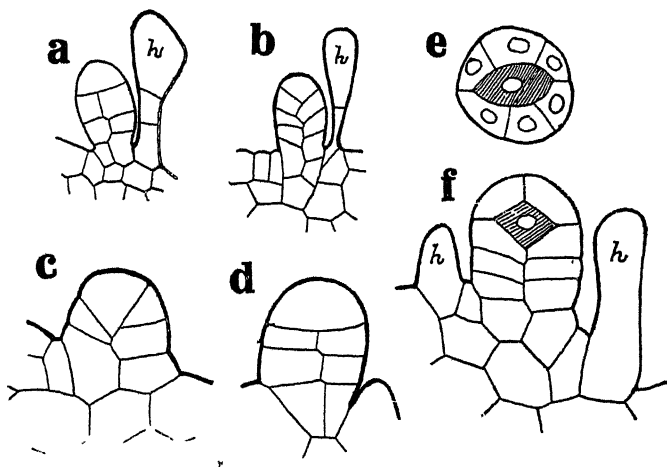


FIG. 353.

Illustrations of two-sided segmentation of Fern sporangia. *a, b*, of *Cheiropleuria*, showing aspects at right angles to one another. $\times 165$. *c, d*, the like for *Metaxya*. $\times 200$. *e*, a rather older sporangium of *Metaxya* seen from above; *f*, seen from the side. *h, h* = hairs. $\times 200$.

pleuria (Fig. 353, *b, e, f*), and it is frequent in Cyatheoid Ferns. Analogies with these types of cleavage will readily be found in the apical segmentation of vegetative parts, whether axes or leaves. In either case the four-, three-, or two-sided cleavages are related respectively to the symmetry, and to the greater or less bulky development of the part in question.

SPORANGIAL STALKS

In some of the Eusporangiate Ferns, such as *Botrychium*, the stalk is a massive column, traversed by vascular tissue (Fig. 326). But it is only in the largest of them that there is any individual vascular supply: in the stalk of *Angiopteris* there is none (Fig. 330), and this is so for all of the Leptosporangiate Ferns. In those of them included in the Simplices the sporangia have usually short stalks; in some of the largest of them the stalk consists of a central column of cells surrounded by a superficial series, as in *Gleichenia circinata*, and sometimes in *Osmunda* (Fig. 353 *bis, a, d*). In others the central column is represented by a single cell-row (*c, e, f, h*); but in most Leptosporangiates this is absent. The transverse section then shows a radial segmentation as in Fig. 353 *bis, b, i, j, m*, etc.; and this leads by successive steps of simplification to the three-rowed stalk, which is the commonest of all

in Leptosporangiate Ferns (*l, o, p*). But this again may pass into still simpler structure (*n, q*), till finally the stalk comes to consist of but one row of cells

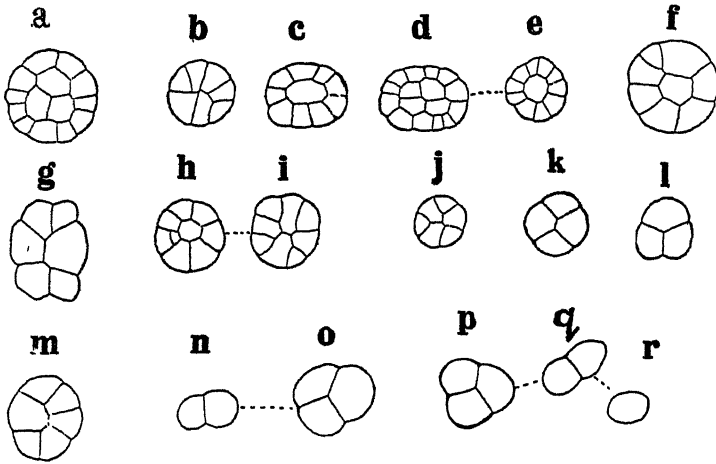


FIG. 353 bis.

Series of transverse sections of sporangial stalks, showing steps of progressive simplification. All are approximately to the scale $\times 150$. *a* = *Gleichenia circinata*. *b* = *Gl. linearis*. *c* = *Mohria*. *d, e* = *Osmunda*. *f* = *Matonia*. *g* = *Loxsona*. *h, i* = *Thyrsopteris*. *j* = *Cibotium culcita*. *k* = *Metaxya* and *Cheiropleuria*. *l* = *Platyserium*. *m* = *Plagiogyria*. *n, o* = *Elaphoglossum latifolium*. *p, q, r* = *Hypoderris Brownii*. *r* = *Asplenium Trichomanes*.

(*r*), a state found in the most advanced types (compare Fig. 352). A comparison of these figures, which were drawn all to the same scale, shows that the structural complexity is not directly determined by size, though the

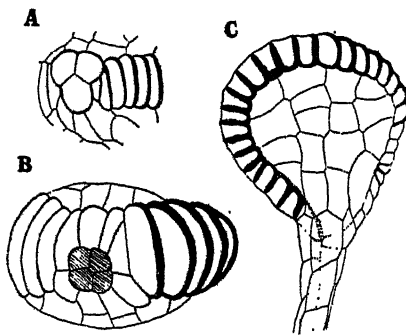


FIG. 354.

A = base of a sporangium of *Pteris grandifolia*, showing the interruption of the annulus, by the insertion of the three-rowed stalk. *B* = base of a sporangium of *Cheiropleuria*, showing the ring continuous, and the 4-rowed stalk. *C* = sporangium of *Platyserium*, showing the ring of the annulus almost interrupted, though still continuous. In *A, B* the distal face is directed upwards; in *C* it is turned away from the observer.

thicker stalks are roughly proportional in section to the bulk of the sporangia, and to the numerical output of spores. (See Tables, p. 426-7.) The stalks of the sporangia with three-sided cleavage are usually three-rowed, or less: as in *Dryopteris* or *Pteris* (Fig. 354, *A, C*); but those of sporangia with two-sided cleavage are usually four-rowed, as in *Metaxya*, the Cyatheaaceae; and in certain Dipterids, such as *Cheiropleuria* (*B*).

The length of the stalk varies greatly: in the Eusporangiates it is consistently short, but in less degree in the Osmundaceae, Gleicheniaceae, Schizaeaceae, Hymenophyllaceae, and Matonineae. In those derivative series which make up the mass of the Leptosporangiate Ferns, where a

aceae, Schizaeaceae, Hymenophyllaceae, and Matonineae. In those derivative series which make up the mass of the Leptosporangiate Ferns, where a

"mixed" sorus is prevalent, the stalk is long, and in extreme cases may consist only of a single row of cells. Such stalks lengthen rapidly as the sporangium ripens, a condition favourable for liberation of the spores when mature; particularly is this so where the receptacle is flat and crowded. Thus, speaking generally, short thick stalks are primitive and long thin stalks derivative and specialised.

THE SPORANGIAL HEAD

A normal type for Leptosporangiate Ferns is presented in the excellent diagram of the sporangium of *Dryopteris* by Kny. It shows the two opposite faces of a slightly compressed capsule of a medium advanced state, while between them is a drawing of the same capsule seen from above, with the respective sides facing right and left (Fig. 355, 3, 4a, 4b). The two faces are not identical in structure, nor in their relation to the cell-rows of the stalk. As a matter of fact they have had a different history, which can only be understood by comparison with more primitive types. That shown as (4a) may be called the *distal face*: that seen as (4b) the *proximal face*. Those two faces present tabular cells forming the single layer of the wall; but the number and grouping of the cells is not the same on both faces. The margin of the flattened capsule is occupied by the *annulus*; about three-quarters of its cells are indurated on their three inner walls, and form the mechanical spring for ejection: this is firmly attached at one end to the sporangial stalk; the remainder of the cells are relatively thin-walled, including a group of four transversely elongated sister cells forming the *stomium*, between the inner pair of which the actual rupture takes place. A pair of thin-walled cells adjoins the stomium on either side, one pair forming contact with the free end of the spring (epistomium), and the other with the sporangial stalk (hypostomium) (Fig. 356). The actual number of cells forming the annulus and its constituent parts varies among Leptosporangiate Ferns, but the mechanism is the same for them all, and the dehiscence appears transverse, or "brevicidal." This contrasts with the longitudinal dehiscence in *Angiopteris*, *Osmunda*, *Gleichenia*, or *Schizaea*, which has been styled "longicidal" (Von Goebel). An intermediate state is, however, present in gradate sori, where the dehiscence is oblique, as in the Hymenophyllaceae and Cyatheaceae.

It has been seen how in *Etapteris* (Fig. 295), *Corynepteris* (Fig. 296), and *Angiopteris* (Fig. 330) a mechanical band forms an arch over the apex of the sporangium, descending as a broad tract of indurated cells down either side. It has also been seen how in *Todea* (Fig. 332), and *Mohria* (Fig. 339, D, E) the mechanical tissue is closely grouped round the distal end of the sporangium. In the latter it may well be that, so far as there is any strict homology between them, this more restricted area is the correlative of the more extensive arch of

the former types. The Schizaeaceous fossil *Senftenbergia* (Fig. 340) would from this point of view present an extreme result of such restriction, its mechanical tissue appearing as a compact distal cap. But there is no need to insist on such comparisons: it is quite possible that the mechanisms in plants so distinct may have been homoplastic in origin. Putting them therefore aside, a compact type, as seen in the Osmundaceae and Schizaeaceae, may

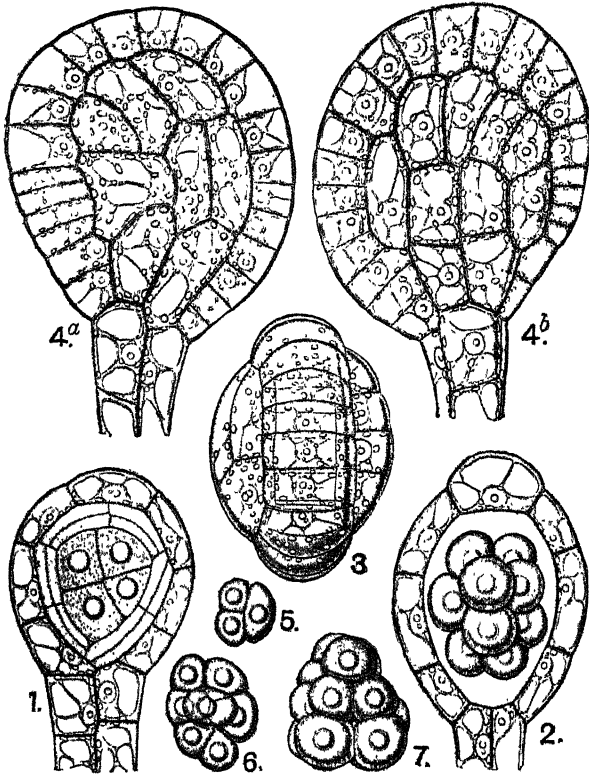


FIG. 355.

Later stages in the segmentation of the sporangium of *Dryopteris filix-mas*, after Kny. 4a presents the "distal" face of the capsule, while 4b presents the "proximal." In 3 the distal face is to the left, the proximal to the right. Thus a single row of cells of the stalk leads up to the proximal face, while the other two form the base of attachment for the ends of the annulus, which are here separate.

well have been a starting point in the evolution of the more specialised annulus seen in the Leptosporangiate Ferns. Within this more restricted field steps may be traced leading towards their more simple but more exact annulus, and to the development of the distal face which it surrounds.

The area of thin-walled cells, styled the "plate" or "distal face" of the sporangium, was shown by Prantl to vary in the different genera of the Schizaeaceae (Fig. 339). In *Mohria*, as also in *Todea*, the apex is occupied only by indurated cells (*D*). In *Schizaea* the plate appears only as a single

cell (Fig. 342, *C*); but in *Anemia* it forms a circular distal area consisting of numerous thin-walled cells, while the annulus is a single horizontal ring of cells surrounding it (Fig. 342, *D*). This plate appears as an increasingly important feature in the pear-shaped sporangia of many other relatively primitive Ferns. For instance, in the Hymenophyllaceae, in *Loxsomopsis*, *Thyrsopteris*,

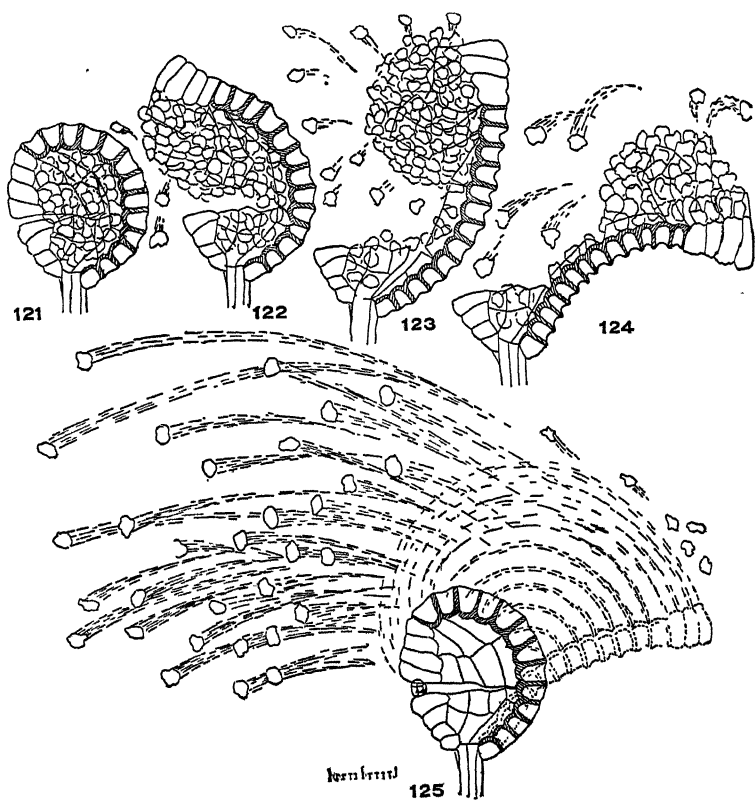


FIG. 356.

Dispersion of the spores from the sporangium of *Polystichum* (*Aspidium*) *acrostichoides* showing stages in the eversion and snapping of the annulus. (After Atkinson.)

Cibotium, *Plagiogyria* (Fig. 357, *c*), *Gleichenia* (Fig. 357, *b*), *Lophosoria*, and in *Matonia*; appearing as an area more or less completely circumscribed by the annulus of the pear-shaped sporangia. Comparison thus suggests that there has been a general expansion of the mechanical tissue, together with its fining down to a single ring of effective mechanical cells, which surround an enlarging plate of delicate tabular cells. A necessary condition for the mechanical action of the uniseriate annulus is that it should be connected not only with one but with two tracts of thin-walled tissue. The initial stages in such a progression are not likely always to have been preserved, but they are indicated in the Schizaeaceae.

Successful dehiscence by means of a mechanical ring requires free space beyond that occupied by the ripe capsule itself: it may take the form of lateral elbow-room or of free space overhead. As the sporangia multiply—which they are seen to have done in many advancing evolutionary lines—soral crowding will be the result, and a condition of mechanical deadlock may be reached. This has already been noted in the case of *Gleichenia* (Figs. 348-9). It has been seen in Chapter XVIII how such difficulties have been met in various types of Ferns by modification of the form of the sorus,

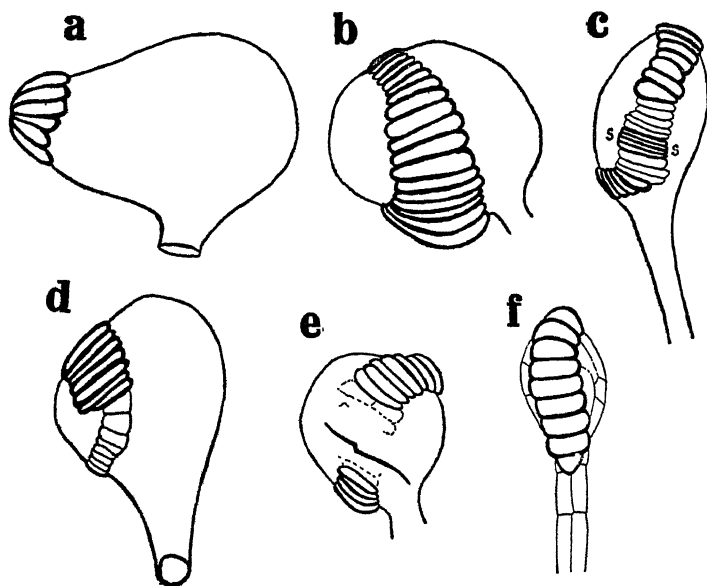


FIG. 357.

Sporangia of various Ferns orientated so that the distal face is to the left, and the proximal to the right. This brings clearly into view the differences in proportion of those faces, and of the position of the annulus and stomium. *a*=*Lygodium*; *b*=*Gleichenia*; *c*=*Plagiogyria*; *d*=*Loxsoma*; *e*=*Hymenophyllum*; *f*=*Leptochilus*. *s*, *s*=stomium.

and by the introduction of a sequence of sporangia, whether gradate or mixed, borne upon an elongated receptacle. Here the point of interest will be the modifications seen in the sporangial head, and particularly of the annulus in relation to these changes. They are suggested broadly by the drawings of actual sporangia presented in Fig. 357. To aid their comparison they are all orientated so that the distal face is turned to the left. All these illustrations show a single-rowed annulus of advanced type. The differences of form depend chiefly upon the varying proportion of the distal and proximal faces, and of the position of the annulus in relation to them. Further, the curvature of the capsule itself plays an important part, while in relation to these features the position of the slit of dehiscence varies also. In *Lygodium* and *Schizaea* the distal face is small in area, but the proximal is distended,

giving the sporangium an ovoid form, with a cap-like annulus at the apex (Fig. 357, *a*). The dehiscence is "longicidal," by a median slit (Fig. 342, *a, c*). But if the distal face were enlarged so as to form a considerable convex area, and the annulus were dilated so as to form a zone running obliquely round the body of the sporangium, the type of *Gleichenia* would result, though still with the same constituent parts, and with the dehiscence in a median longitudinal plane (Fig. 357, *b*). A slight difference in proportion, but with only partial induration of the annulus, gives the sporangium of *Loxsonia*, the only known Fern with a gradate sorus and median longitudinal dehiscence (*d*).¹ In other Gradate Ferns, and in all the Mixtae the dehiscence is lateral, designated by Von Goebel as "brevicidal." In the least modified of these the annulus still remains as a complete ring, and the stomium lies at the side, the slit being oblique, as in *Lophosoria*, *Dicksonia*, *Hymenophyllum* or *Plagiogyria* (Fig. 357, *c, e*). But in the Mixtae, where the sorus is crowded, and the receptacle usually flat, the annulus tends to the vertical position, though often with some degree of bias, and the dehiscence is transverse (Fig. 357, *f*). This is the state seen in *Dryopteris*, or in *Pteris* (Fig. 354, *A*): it is the typical "brevicidal" dehiscence of Von Goebel. Here the annulus is seen to be more or less completely interrupted by the insertion of the stalk; but in *Cheiropleuria*, and not a few other Ferns, the annulus may still be traced past the insertion of the chain of cells of the stalk (*B*).

The biological fitness of such variations of the sporangia in relation to the structure of the sorus is worthy of remark. The median dehiscence in the simple radiate sorus of *Gleichenia* is as effective as it is in those Eusporangiate types where the sporangia are free; but here there is a single ring of mechanical cells except for occasional duplication, which as in the sporangia of the Schizaeaceae points to a more complex ancestry. Even in *G. linearis*, where one or more sporangia occupy the centre vacant in most species, it is still practicable (Fig. 348). But the mechanical difficulty, following on median dehiscence, already appears in the crowded sorus of *Gleichenia pectinata* (Fig. 349). A slight modification of the annulus, widely adopted by gradate Ferns, meets the difficulty, viz., the lateral dehiscence. That this is not necessarily associated with a gradate state is shown by its very perfect development in the long-stalked sporangium of *Plagiogyria* (Fig. 357, *c*). But the constancy of its occurrence in gradate Ferns, and finally in those with mixed sori, is evidence of its biological value. This will be clear from the diagram for *Trichomanes* (Fig. 310). Here the receptacle is elongated, bearing a long basipetal succession of short-stalked sporangia, protected till ripeness by a basal cup-shaped indusium, as already described in Chapter XVIII, p. 376. Free head-room for the eversion of the annulus is secured by the elongation of

¹ For an explanation of this unique state, in terms of other genera, see *Ferns*, vol. ii., p. 255.

the receptacle, and full advantage is taken of it as a consequence of the lateral dehiscence in place of the median.

It is in the crowded sori of the Mixtae that the dehiscence becomes fully "brevicidal," and the slit of dehiscence transverse. In the transitional state from a simple or gradate sorus to the mixed type, as seen in several distinct phyla, intermediate conditions may be found between the longicidal and the brevicidal types of the sporangia. A number of instances may be cited where the induration of the annulus ceases at the insertion of the stalk, though the sequence of cells of the ring is continued past it : as in *Lindsaya*, *Dipteris*, and *Cheiropleuria* (Fig. 354, *B*) ; or the chain of its cells may be actually interrupted, as in *Leptochilus* (Fig. 357, *f*), or *Pteris* (Fig. 354, *A*). The delicate gradations seen between the complete ring of the annulus and its actual interruption form a chain of evidence which, when related to the change in soral constitution, suggests steps in a progressive advance from a complete indurated ring with oblique dehiscence, as in *Hymenophyllum* or *Cibotium*, to an interrupted ring with transverse dehiscence, as in *Pteris* or *Dryopteris*. This, combined with the elongation of the stalk which lifts the mature capsule above its fellows, will allow the annulus to be everted outwards, using the free space overhead. But the biological advantage of the mixed sorus, combined thus with modification of the sporangial head, is not confined to the facility for dehiscence. It allows of a long continued period of spore-production, and at the same time provides for the protection of the very young sporangia. This is assured partly by the older sporangia still maturing, partly by the persistent stalks of those which have already dehisced ; but partly also by hairs which frequently fill the interstices so as to enfold the critical stages of youth (Fig. 313). These biologically important results are aided by a vertical annulus with transverse dehiscence : an approach at least to that state seems to be a necessary condition for their success.

The foregoing paragraph has been written so as to present and correlate the bare facts with functional results. There have been two views put forward in explanation of the apparent *change of position of the annulus*, in relation to the whole capsule, involved in the comparison of the transverse and the oblique with the vertical position, and of the longicidal with the brevicidal dehiscence. The facts have been held by some to suggest that there has been, in a plurality of phyletic lines, an "actual swing" of the annulus from a primitively transverse position, as in the Schizaeaceae, to the oblique, and finally to the vertical position, with the consequence that the dehiscence has changed from the longitudinal, through an oblique, to a transverse plane. This view was based upon a somewhat rigid comparison of the sporangia as parts having a certain structure, but subject to differences of proportion. An "actual swing" of the annulus was attributed to a gradual displacement, the stages of which were held to be reflected in sequences taken from the various distinct phyla of Ferns quoted and compared. This was stated in *Ferns*,

vol. i., p. 256.¹ Professor Von Goebel has expressed his dissent from this interpretation, which will be best conveyed by quotation.² "An 'actual swing' of the annulus in the different forms of sporangium independent of a change of their general symmetry, a *gradual* displacement the various stages of which are partially retained in the different groups of Ferns, appears to me now as improbable as before. If we assume that dorsiventral sporangia were the primitive forms whence all others arose, one may further presume that from these were derived those which possess another type of symmetry. But I see no decisive grounds for the assumption that in the derivatives the ring should have been gradually displaced from an oblique to a vertical direction. It is true a series may be arranged in which the different positions of the ring are demonstrated. We apprehend that this position did not result from a gradual change, but was *present from the first*. It forms a part of the general characteristic of the several groups, which in our view originated polyphyletically. They arose from a more or less fundamental change in the individual groups brought about in the general symmetry of their sporangia by the inherent properties of the archespore."

This last sentence introduces a new factor into the problem of sporangial form and structure, viz., the relation of the archespore to the general symmetry of the sporangium, and in particular to the position of the annulus and of the stomium. In elucidation of this certain of Von Goebel's drawings are quoted as Fig. 358. They suggest for those sporangia which have a tetrahedral archespore that a definite relation exists between this and the stomium. In Fig. 358, 207, 208, the point marked (*st*) represents the line of dehiscence: it lies opposite the middle of that side of the archespore marked (*x*, *x*). From that the line of the annulus may be inferred. As an example *Pteris longifolia* has been chosen, and the substance of the following description has been taken from Von Goebel's text (p. 194). The originally tetrahedral archespore soon loses that form; but, if we assume it as persisting, then the stomium is opposite one lateral face of the tetrahedron (Fig. 358, 207). This falls behind in growth, while the other three faces become elongated (208). Thus, after division of the archespore, a sporogenous cell-complex arises orientated obliquely to the longer axis of the sporangium, but with its flattened surface turned towards the stomium. This is often clearly shown in transverse sections of the older sporangia, as it is in Fig. 358, 210, where the spore-mother-cells are separate and rounded. The section through a cell of the annulus is recognised by its size (*A*). The spore-mother-cells form a triangular group with its base directed to the stomium, its apex to the annulus. From these and other observations the conclusion may be drawn that the orientation of the archespore in the Polypodiaceae is definitely related to the initiation of the annulus and stomium, while the first tapetal cell cut off from the archespore lies on the side where later the stomium appears (*l.c.*, p. 197).

There, as regards facts, we must leave this line of enquiry. The confirmation of the conclusions of Von Goebel will demand further observation, *particularly in relation to the varying form of the archesporial cell, whether cubical,*

¹ A summary is there given of the results acquired in "Studies in the Phylogeny of the Filicales," i.-viii., *Ann. of Bot.*, 1910-1923.

² *Buit. Ann.*, xxxix., 1928, p. 199; also *Organographie*, 1930, ii., p. 1353.

tetrahedral, or two-sided. It may be a question whether his suggestion will apply equally to them all; and if so how does the detail work out? The interest may well centre upon *Todea* as a test case, owing to its fluctuation between a cubical and a tetrahedral form of the archesporium: or upon those Ferns already quoted where it is two-sided (Fig. 353). Meanwhile it may be held in doubt whether the actual form of the archesporial cell will prove to be one of those inherent properties of the archesporium to which the fundamental changes have been referred; such influence as it exercises may possibly be

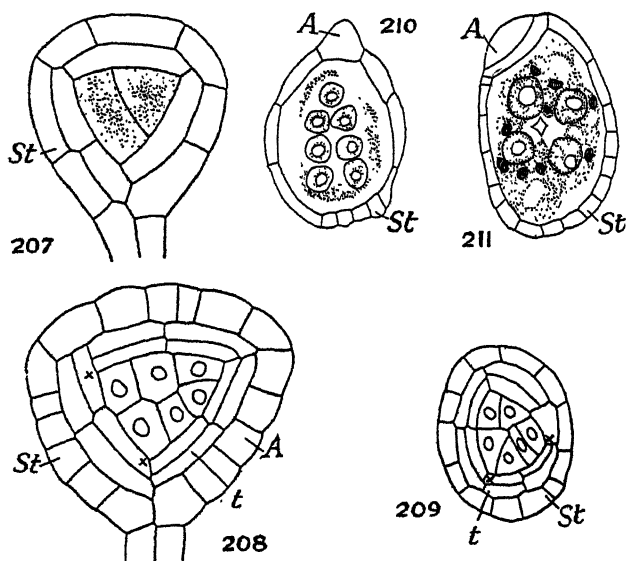


FIG. 358.

Pteris longifolia. 207, young sporangium in longitudinal section. The archesporium dotted; *st*, the stomial side (diagrammatic). 208, ditto, an older sporangium; *A*, cells which develop later into the annulus; *t*, tapetum; *x, x*, the tetrahedral surface which, facing the stomium, grows less strongly (diagrammatic).

Pteris cretica. 209, sporangium in transverse section, in a middle-stage of development; *st*=the stomial side: the nuclei are indicated in the sporogenous cells; otherwise the lettering as in 208.

Pteris longifolia. 210, sporangium in transverse section, with isolated spore-mother-cells, suspended in the tapetal periplasmodium. *A*=annulus; *st*=stomium.

Ceratopteris thalictroides. 211, sporangium in transverse section, traversing four spore-mother-cells. Lettering as before. (After Von Goebel.)

independent of its form. A further point is that sporangia with oblique or transverse dehiscence may be either right or left handed: looking down upon the distal face of the sporangium the stomium may lie either right or left. A good example is seen in *Loxsomopsis*,¹ and instances have been seen in other Ferns, e.g., *Matonia*.² This suggests either that the detail of the annulus is not standardised, or that the influence of the archesporium, if any, is variable. Such facts will affect either of the theories above noted.

As regards the evolutionary aspect of the question, the problem stands very much as it was before this interesting correlation was suggested. The statement that it is possible to arrange apparently transitional forms in a

¹ *Ferns*, ii., Fig. 524.

² *Ibid.*, ii., Figs. 500, 501.

sequence, but that the result does not necessarily bear any evolutionary significance, might have weight if there were only one such sequence. But like changes have been seen to appear in a plurality of sequences of naturally related genera and species, in which phyletic advance has been shown not only in this but in other independent characters. The interruption of the annulus, partial or complete, at the insertion of the stalk, which has been seen in a plurality of lines of recognised kinship, can hardly be set down to any other cause than "gradual change." It is hardly credible that these differences were, as Von Goebel holds, "present from the first." So long as the influence ascribed to the archesporium is as indeterminate as it appears to be at present, the effects observed do not justify the ruling out of the general comparisons which have been here advanced, but may rather add to the sum of them one still more intimate. Hence, it may be held that the question of what determines causally the form of oblique or brevicidal sporangia, and the position of the stomium and annulus, is still in the air. But the suggestion of a relation of the archesporium to such results has certainly opened a new chapter of this discussion.

THE SPORE-OUTPUT PER SPORANGIUM

The output of spores from each sporangium in Ferns accords generally with their structure. As a consequence it is found that the number of spores per sporangium will give an additional basis for their comparison. This method was first suggested by Russow, and enumerations were carried out by him in some few cases¹; but it is only recently that countings of spores have been so far extended as to make the spore-output a useful accessory to general comparison. Among the fossils this method has proved of great value in confirming conclusions based on other grounds. A census of the spores of a single sporangium may be made by direct counting where the numbers are low; but for large numbers this is tedious, and cannot be very accurate: in such cases an approximate estimate may be formed by examination of transverse and longitudinal sections in the stage of the spore-mother-cells. The results by either method are found to be approximately constant for the individual or species, or even for the genus or family, particularly in the more precise sporangia of the Leptosporangiate Ferns. Nevertheless, as will be shown later, some striking divergences do occur, which are sometimes susceptible of biological explanation. The numbers range from thousands of spores in the Eusporangiate Ferns down to a single matured spore in the megasporangia of the Hydropterids. In the great majority of cases the numbers centre round powers of two: 8, 16, (24), 32, (48), 64, 128, 256, etc. This points obviously to a process of repeated bi-partition of the cells of the sporogenous group, terminated by the usual tetrad-division. The figures 24 and 48 do not fall into the direct series, though they are not uncommon. The number 48, seen in the Male Shield Fern, probably results from the

¹ *Vergleichende Untersuchungen*, 1872, p. 86.

division of the archesporium into 2, 4, and 8; only four of the resulting cells would then undergo the next division, giving 12 spore-mother-cells, and consequently 48 spores. (See Fig. 355.) A similar process stopping one step earlier would give the number 24. The figures 32, 16, and 8 result from earlier arrest of bi-partition.

A first table relating to the Simplicies illustrates the higher numbers, and comparison of these with the several sporangia of the plants named will show how far structure runs parallel with output. The results, whether of estimate or from actual counting, are stated in "typical numbers"; by this is meant those powers of two which lie next above the highest actual counts or estimates for the plant named. Since observation shows, especially in the largest sporangia, that all the spore-mother-cells do not mature their full tale of spores, this mode of statement will be sufficiently accurate for purposes of comparison. In a much more elaborate table given in *Ferns*, vol. i., p. 262, the actual results of countings are given for a larger number of genera and species than those here quoted.

TABLE FOR SELECTED TYPES OF THE SIMPLICES

<i>Ophioglossum pendulum</i>	-	-	-	-	15,000
<i>Marattia</i>	-	-	-	-	2,500
<i>Danaea</i>	-	-	-	-	1,750
<i>Botrychium Lunaria</i>	-	-	-	1,500 to 2,000	
<i>Angiopteris</i>	-	-	-	-	1,450
<i>Gleichenia flabellata</i>	-	-	-	512 to 1,024	
<i>linearis</i> and <i>pectinata</i>	-	-	-	-	256
<i>Osmunda regalis</i>	-	-	-	256 to 512	
<i>Todea hymenophylloides</i>	-	-	-	128 to 256	
<i>Lygodium dichotomum</i>	-	-	-	-	256
<i>Lygodium pinnatifidum</i>	-	-	-	-	128
<i>Anemia phyllitidis</i>	-	-	-	-	128
<i>Schizaea malaccana</i>	-	-	-	-	128

These examples of the Simplicies are arranged according to spore-output, and the three at the top are all synangial. This does not necessarily point to their being the most primitive; probably the high figures result from some advantage in spore-production which follows from a secondary fusion, rather than an independent development of the sporangia. *Botrychium* and *Angiopteris* present a numerical output between 1,000 and 2,000, which appears to be normal for the latter state in both families. The genus *Gleichenia* presents in *G. flabellata* an approximately equal number, but in those species where the sporangia are more numerous and smaller the output from each is less. A like fluctuation but in lower figures is seen in the Osmundaceae, where the Royal Fern almost tallies with *G. flabellata*, but the filmy *Todea hymenophylloides* gives only 128 to 256, probably in relation to its filmy habit. A similar fluctuation appears within the genus *Lygodium* with 256 to 128, while the rest of the Schizaeaceae fall under the typical number of 128. Apart from actual size, those sporangia where numbers are above

1,000 often have more or less definite vascular supply, while those below that figure have not. The sporangial wall and tapetum are also more massive in the former, and this is seen in minor degree in *Osmunda* (Fig. 335), and *Lygodium* (Fig. 344), as compared with the usual Leptosporangiate type of structure.

In the vast majority of the Leptosporangiate Ferns each capsule contains 64 spores, or less. But there are a few exceptions where the number is greater; they may be tabulated thus:

TABLE FOR INTERMEDIATE TYPES

<i>Hymenophyllum tunbridgense</i>	-	-	256 to 512
„ <i>sericeum</i>	-	-	256
„ <i>Wilsoni</i>	-	-	128
<i>Trichomanes reniforme</i>	-	-	256
„ <i>radicans</i>	-	-	48 to 64
„ <i>pinnatum</i>	-	-	32 to 48
<i>Cheiropleuria bicusps</i>	-	-	128
<i>Jamesonia scalaris</i>	-	-	64 to 72

Such infrequent exceptions possess a special interest. The sporangia of the Hymenophyllaceae present a more variable spore-output than those of any other family; but the number of their spores runs fairly parallel with the size of their sporangia. The higher numbers found in certain species, whether of *Trichomanes* or of *Hymenophyllum*, approach those in the Simplices, while the lower numbers may be held as evidence of the advanced hydrophytic adaptation of the species where they are present, and suggest that this gradate family, which has anatomical features like those of the Botryopterids, with Sphenopterid foliage, represents an ancient stock biologically specialised and reduced. The case of *Cheiropleuria* is similar: its probable relation is with the Dipteroid fossils of the Mesozoic period, in which such numbers have been found as 128 (*Thaumatopteris*), or even 512 (*Dictyophyllum*).¹ The case of *Jamesonia*, where the spore-counts only slightly exceed the normal for Leptosporangiate Ferns, is less easily intelligible.

In the great mass of Leptosporangiate Ferns the typical numbers are 64, 48 and 32; but in some genera a wide diversity appears. For instance, while *Alsophila* regularly approximates to 64, *Cyathea* varies from 64 in *C. medullaris* to 16 or even 8 in *C. dealbata*. *Pellaea falcata* has 64 as against 24 in *P. hastata*. *Cheilanthes Fendleri* has 64 as against 32 in several other species. *Notholaena trichomanoides* has 48 as against *N. sinuata* with 32, 24, or 16. Lastly *N. affinis* bears sporangia either with 64 small spores or 12-24 large spores; and a like variability in size appears in *Platysoma* (32-16), and in *Ceratopteris* (32-16). Where the spores differ in number in relation to size there is an obvious suggestion of incipient heterospory, a state

¹ H. H. Thomas, *Proc. Cam. Phil. Soc.*, 1922, p. 109.

not yet proved for them, but fully realised in the Marsiliaceae (64-1) and the Salviniaceae (64-1). Such differences often go with divergence in size of the sporangia, or with marked specialisation of megasporangia, as in the Hydropterids.¹

Notwithstanding the progressive fall in the spore-production of the individual sporangium which these comparisons indicate, the output per sorus may remain approximately constant. This may be shown by comparison of Ferns systematically remote from one another. For instance, the estimated production of spores per sorus for *Marattia fraxinea* is 45,000, for *Phlebodium aureum* 57,000 :— for *Angiopteris evecta* 14,500, for *Hymenophyllum dilatatum* 11,500 :— for *Alsophila excelsa* 3,200, for *Gleichenia flabellata* 3,000. The similarity in output in such pairs of cases may be set down to mere similarity of the underlying nutritive mechanism. These comparisons become more interesting when the plants compared are of near affinity, as in the Hymenophyllaceae, in which the sorus has a uniform type of construction, though the size and number of the sporangia and the length of the receptacle are variable. The results of their comparison are given in the subjoined table :

NAME.	Sporangia per sorus.	Spores per sporangium.	Output per sorus.
<i>Hymenophyllum tunbridgense</i>	20	420	8,400
<i>Trichomanes reniforme</i> -	40	265	10,600
<i>Hymenophyllum dilatatum</i> -	90	128	11,520
<i>Trichomanes radicans</i> -	140	64	8,960

It thus appears that notwithstanding the great variations of sporangial output the result per sorus is approximately uniform for the cases quoted, which all belong to a very natural family of Ferns. Thus the diminution of output of the individual sporangium does not necessarily lower the productivity of the sorus ; for it is often compensated by the larger number of the sporangia.

TAPETUM AND SPORES

The tapetum is not a morphological constant. In the Ophioglossaceae and Marattiaceae it originates outside the definitive sporogenous group as an ill-defined band consisting of several layers of tabular cells ; but in the smaller sporangia of Leptosporangiate Ferns it is cut off from the archesporium itself. A parallel to this is seen in the large sporangia of *Lycopodium*, where it originates outside the sporogenous group, while in the smaller sporangia of

¹ See *Ferns*, vol. i., p. 262-3, where many enumerations are given.

Selaginella it is derived from the superficial cells of the group. The difference may thus be correlated with size. As the spore-mother-cells round off prior to tetrad-division the tapetal cells fuse to form a plasmodium, their nuclei often undergoing fragmentation. The plasmodium intrudes between the separating spore-mother-cells, forming a rich nutritive medium, which is absorbed in the more primitive Ferns into the developing spores; but in certain advanced types it may in part remain as a deposit on the outside of the wall, and is called the *perispore* (Fig. 359). The wall of the spore itself

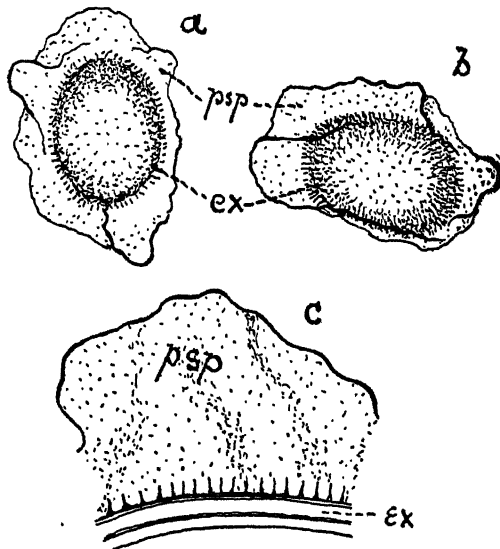


FIG. 359.

Spores of *Aspidium trisophatum*, after Hannig. *a*, *b*=ripe spores with prickly exospore (*ex*), and transparent perispore (*psp*), appearing like a loose sac ($\times 500$). *c*=part of the exospore and perispore more highly magnified.

is often marked by characteristic sculpturing which at times gives a basis for systematic comparison; but in this the perispore is more important. Ferns may in fact be divided into two groups according to the presence or absence of a perispore. None is seen in the Eusporangiate Ferns, nor in the Osmundaceae, Schizaeaceae, Hymenophyllaceae, Cyatheaceae, Davalliaceae, or in *Ceratopteris*. In fact, it is absent from all the more primitive Ferns, and of the remaining Leptosporangiates it is wanting in the Vittarieae, Gymnogrammeae, Polypodiaceae, and Pterideae; but it is present in the Asplenieae and Aspidieae. The perispore thus possesses a certain value for comparison; but confidence in it as a safe criterion is shaken by the fact that while it is present in *Blechnum* and *Woodwardia* it is absent in the closely related *Brainea* and *Doodya*. It is clearly a feature adopted late in descent, and restricted to certain circles of affinity.

There are two main forms of spores in Ferns : the wedge-shaped or two-sided, and the three-sided or tetrahedral (Fig. 360). The former results from the division of the spore-mother-cell by three cleavages to form spores with

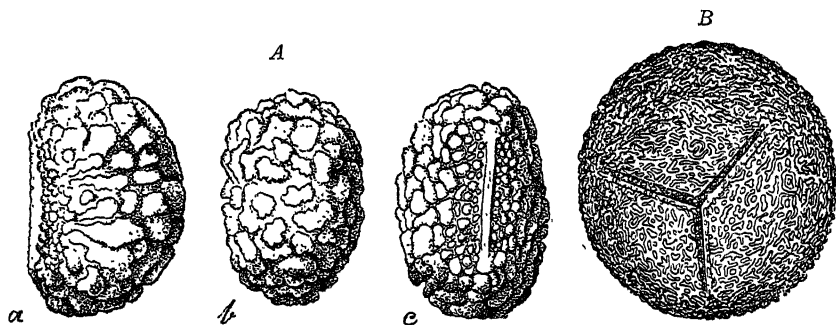


FIG. 360.

A=spores of *Polygodium vulgare*, showing the wedge-shaped, two-sided form of spore from three aspects. B=spore of *Osmunda regalis*, of tetrahedral form. $\times 444$. (After Luerssen.)

two flattened sides (A) ; the latter results from division by six walls so disposed as to give the spores a tetrahedral form (B). Both of these may occur within nearly related circles ; for instance, the Marattiaceae and Schizaeaceae include both types : thus the spore-form also is an uncertain guide to affinity.

HETEROSPORY

It has been seen how in certain Ferns there is a marked difference between spores of the same species, whether in number or in size. *Notholaena* and *Platyzoma* have served as examples (Fig. 361). But in the Marsiliaceae and Salviniaceae such differences are more pronounced, and they are definitely related to a distinction of sex. Notwithstanding the extreme specialisation of

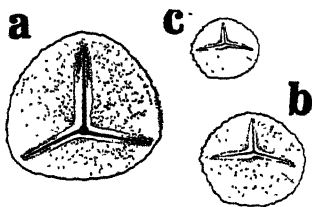


FIG. 361.

Spores of *Platyzoma*, after McLean Thompson, all drawn to the same scale. a=one of the largest ; b=of medium size ; c=one of the smallest. $\times 26$.

these Hydropterids (for the details of which reference should be made to special treatises) they are clearly referable to a Leptosporangiate source, as is shown by many features both vegetative and propagative. For instance, in *Azolla* the sporangia arise by growth and segmentation of the type usual for Leptosporangiate Ferns : they are associated in sori showing evidence of a gradate sequence, and are surrounded by a flask-shaped basal indusium. The microsporangia are numerous in each sorus, and the number of their spore-mother-cells is 16. These on tetrad-division would give the usual Leptosporangiate number of 64 spores, all of which normally develop as microspores. Only a single megasporangium is borne in each mega-sorus, though a gradate sequence of abortive sporangia may be seen below it. The spore-

mother-cells are here 8 in number : only one of these undergoes tetrad-division, and only one megaspore is matured from that tetrad. The tapetal development plays an important part biologically. In either type of sporangium there is the usual double layer of tapetal cells, which merge into a nucleated plasmodium. Thus far this accords with the Leptosporangiate type ; but in *Azolla* the further development has a peculiar relation not only to sex-differentiation but also to the aquatic habit. In the microsporangia the contents separate into a number of "massulae," each of which consists of a clump of periplasm including many microspores. These are set free separately into

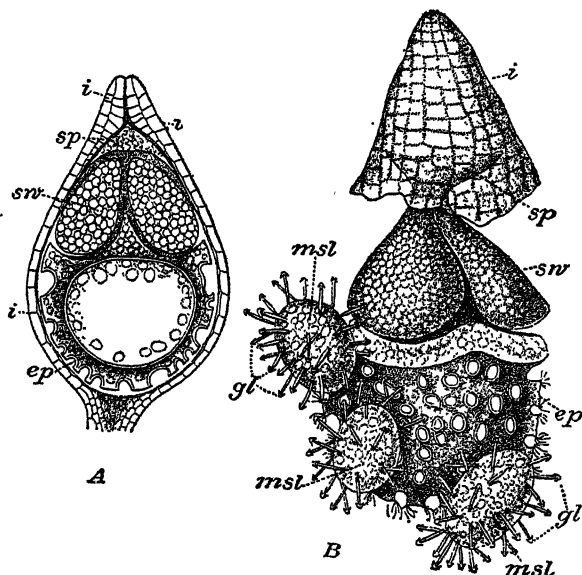


FIG. 362.

Megasporangium and megaspore of *Azolla filiculoides*. *A* shows a megaspore in longitudinal section surrounded by the complete indusium. *B*=a megaspore suspended in the upper half of the indusium; the massulae (*msl*) are attached firmly by their glochidia (*gl*) to the episore, with its many fine hairs; *i*=indusium; *ep*=episore (=perispore); *sw*=swimming apparatus; *sp*=residue of the sporangial wall, which in *A* still covers the swimming apparatus within the apex of the indusium; in *B* it has assumed a funnel-shape. $\times 75$. (After Strasburger from Engler and Prantl.)

the water, and being provided with anchor-like processes (glochidia) they attach themselves to the rugged surface of the megaspore (Fig. 362). This is a body of large size, which has been set free at maturity by rupture of the indusium and obliteration of the sporangial wall: it is oval-tetrahedral in form, and is covered first by its own wall, outside of which is a rugged perispore. The whole may represent the equivalent of one female massula, while its apex is surrounded by three other vacuolated bodies, probably corresponding to the other three aborted megaspores of the fertile tetrad, together with their periplasm. However peculiarly specialised these bodies may appear, they are all intelligible in terms of the Leptosporangiate type, the perispore taking a prominent part biologically in relation to the 64 microspores and to the solitary megaspore. An opening mechanism is entirely absent, the

spores being set free by disorganisation of the sporangial wall, and of the indusial covering. These details are briefly stated here to show that even this highest elaboration of the sporangium and its contents is referable in origin to the ordinary Leptosporangiate type.

DEHISCENCE

The dehiscence in the advanced Leptosporangiate Ferns is exemplified by the sporangia of the Male Shield Fern (Fig. 363). The vertical annulus is here a highly developed cohesion-mechanism. The active cells have their walls thickened on the three inner sides, while the peripheral wall remains thin (*D*). The cell-cavity is filled with sap, which is liable to evaporate on ripeness with diminution of volume. The thin peripheral wall is thus sucked gradually inwards, owing to the adhesion of the shrinking liquid to the wet cell-wall; and the thickened lateral walls are drawn together, which

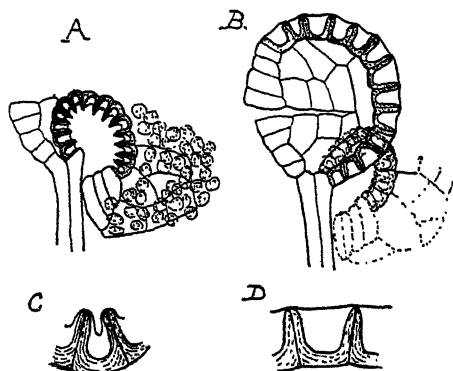


FIG. 363.

Dehiscence of a sporangium. *A* = sporangium with annulus everted. *B* = a similar sporangium after recovery by a sudden jerk. *C* = condition of cells of the everted annulus. *D* = cells of the annulus before eversion, and after recovery.

causes in them a condition of strain (*C*). The result of this is not only to rupture the stomium but also slowly to evert the ring (*A*). As the evaporation continues the increasing strain on the deformed walls overcomes the internal cohesion of the sap, and a vacuum is formed suddenly and simultaneously in many of the cells of the annulus: the result is a sharp jerk of recovery, and ejaculation of the spores, most of which had been already carried outwards on the everted

tip of the capsule (*A*, *B*). This, which is the usual behaviour in Leptosporangiate Ferns on dehiscence, is a highly elaborated mechanism suitable for their delicate structure and crowded habit. Only the indurated part of the annulus is involved, and there is no demand for space laterally, but only distally, for an effective discharge.

In the more massive longicidal types the dehiscence is less highly specialised: it differs in the synangial forms from those where the sporangia are free. Naturally where they are fused no active change of form of the sporangium is possible, and the longitudinal stomium gapes owing to shrinkage of the adjoining cells. This is seen in *Ophioglossum*, *Marattia*, *Danaea*, and *Christensenia*. But where the sporangia are free, opening may be aided by a mechanical annulus, as in *Angiopteris* (Fig. 330). The mechanism has

been above described as passive (p. 397) ; but Von Goebel records ejection of the spores, though not so forcibly as in the Polypodiaceae.¹ He ascribes an active rôle to the mechanical arch. In the more advanced longicidal types the slit, which is defined as in *Angiopteris* by shallow thin-walled cells, is always directed away from the leaf-surface. In the Osmundaceae, Schizaeaceae, and Gleicheniaceae the mechanically thickened annulus tends at ripeness to become externally concave, a result aided by the structure of its cells, and the stomium gapes widely. But there appears to be no forcible ejection of the spores. On the other hand, in the gradate types where the slit is obliquely lateral, and particularly in the Hymenophyllaceae, there is an active ejection (Fig. 310). This highly specialised effect is characteristic of those Ferns in which the annulus consists only of a single row of cells. The single-rowed annulus is in fact a highly specialised derivative from a more massive and mechanically less efficient source.

The general outcome of the comparisons between early Eusporangiate and the later Leptosporangiate Ferns is to suggest a sustained and gradual progression, from bulky and less specialised types of sporangium with individually high spore-output, to delicate and more highly specialised types with individually a low spore-output. Speaking generally, what is lost from the numbers of spores produced in each of the former is made up in the latter by the more numerous sporangia. The physiological drain of production of the spores in the former is simultaneous, in the latter it is spread over a prolonged period, by the adoption of the gradate or mixed conditions of the sorus. The devices for indusial protection during that period are commonly absent in the former, but highly specialised in the latter. The mechanism of ejaculation is quite rudimentary in the former, but is highly delicate and effective in the latter. All these features point in the same direction, and are themselves a biological commentary on the fact, so clearly demonstrated by stratigraphical sequence, that the Eusporangiate are relatively crude and primitive Ferns ; but the Leptosporangiate are derivatives, with their highly specialised methods of the production and distribution of their spores. With few exceptions the Ferns are homosporous, and so depend more directly on numbers of chances than on the advantages which follow on heterospory. The result is that, wherever the conditions on land are suitable for mesothermic hygrophytes, the later and more specialised types form a more prominent feature in the present-day Flora of the Land than do the more primitive Eusporangiates.

l.c., p. 1343.

CHAPTER XXI

THE PROTHALLUS AND EMBRYO OF FERNS¹

THE prothallus of the Filicales found its place early in the history of detailed observation, in contrast to that of the Lycopodiales, of which, as pointed out in Chapter XIV, knowledge came relatively late. In the sixteenth century Valerius Cordus asserted that all kinds of Ferns reproduce by means of dust on the backs of the leaves. Morrison (1699) first raised Fern-plants from spores. In 1788 Ehrhart described the formation of the prothallus, while in 1827 Kaulfuss first observed the germination of the spores. Bischoff in 1842 recognised the embryo attached to the prothallus; Naegeli in 1844 discovered the antheridia and sperms. Suminski in 1848 ascertained the nature of the archegonium, and its relation to the embryo. Finally, in 1851, Hofmeister gave the first complete account of the life-history of a Fern, in his *Vergleichende Untersuchungen*, and he at the same time placed it in relation to that of other Archegoniate Plants. Thus there was no single discoverer of the facts that build up the life-cycle of Ferns; but it was Hofmeister who by his masterly synthesis gave those facts their real significance.

It has been seen in the preceding Chapters how the sporophyte of Ferns provides very varied features for comparison, in respect of external form, internal structure, and propagative organs. Internally it shows a high degree of differentiation, and in particular the vascular system possesses so high a degree of conservatism in its construction that comparisons can effectively be drawn, not only between plants closely related but also between those of wider affinity. In the constitution of their prothallus, however, a much lower scale of differentiation is seen, while its external form, having no regular sequence or relation in parts, is frequently very simple, and is liable to be directly impressed in high degree by the external circumstances under which

¹ *Selected Literature for Chapter XXI (General)*: Von Goebel, *Organographie*, 1930; "Gametophyte," p. 1079, etc.; "Gametangia," p. 1048, etc.; "Embryogeny," p. 1126, etc. Bower, *The Ferns*, vol. i., chap. xiv., "Gametophyte and Sexual Organs"; chap. xv., "Embryo." Vols. ii., iii., *passim*, for special descriptions in various types of Ferns; here the literature is fully quoted. (*Special*): Jeffrey, "*Botrychium virginianum*," *Proc. Can. Inst.*, vol. v., 1898. Lang, "*Scolopendrium*," etc., *Phil. Trans.*, vol. 190 (1898), p. 187. Also "*Helminthostachys*," *Ann. of Bot.*, xvi. (1902), p. 32. Bruchmann, "*Oph. vulgatum*," *Bot. Zeit.*, 1904, p. 227. "*Botr. Lunaria*," *Flora*, 1906, p. 203. Lyon, "*Botr. obliquum*," *Bot. Gaz.*, 1905, p. 203. Campbell, "*Botr. obliquum*," *Ann. of Bot.*, 1914, vol. xxviii., p. 19. *Mosses and Ferns*, 1918, p. 356, for embryology of *Osmunda*, and *passim*, for other types. "*Macroglossum*," *Ann. of Bot.*, 1914. Phillips, "Duration of Prothallia," *Ann. of Bot.*, 1919, p. 265. Land, "Suspensor in *Angiopteris*," *Bot. Gaz.*, lxxv., 1923, p. 421.

it has developed. These facts detract heavily from the value of the gametophyte for comparative purposes, so far as its vegetative characters are concerned ; and we are thrown back upon the sexual organs, or gametangia, as being its most reliable features. Nevertheless, certain somatic characters of the gametophyte may be made use of, and these will be considered first. It should, however, be borne in mind that knowledge of the prothalli of Ferns at large is far less complete than that of the sporophyte, and current views may be subject to revision as the facts are more fully disclosed.

THE CORDATE TYPE

The commonest type of prothallus in Ferns is that of cordate, strongly dorsiventral form, as seen in *Dryopteris* (Fig. 364). It is characterised by the presence of a single growing point, which is distal, being deeply set between

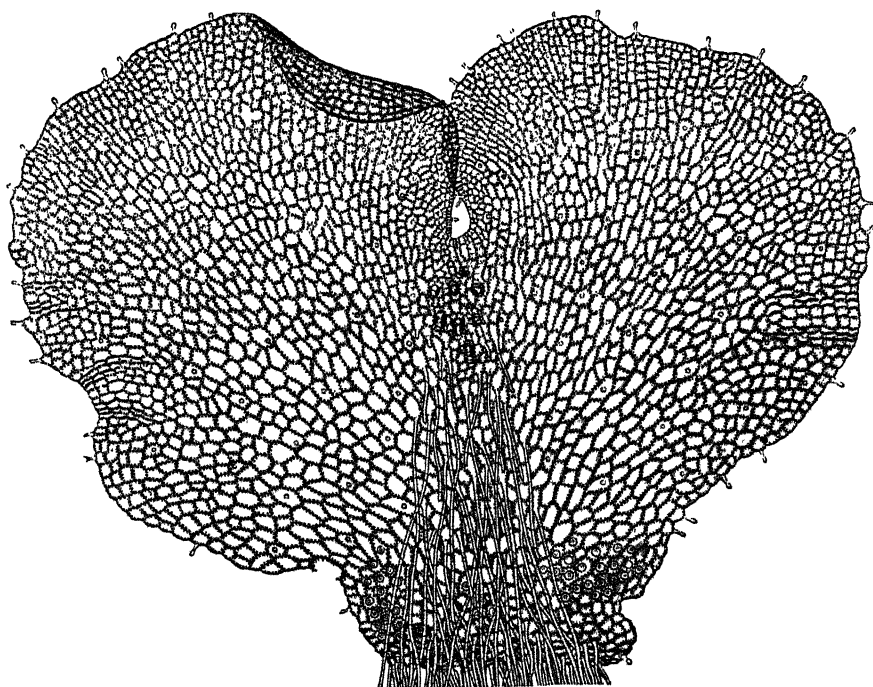


FIG. 364.

Mature prothallus of *Nephrodium filix-mas*, as seen from below, bearing antheridia and archegonia, as an example of the usual cordate form. (After Kny.)

two more strongly growing lateral lobes. Each of these consists of a single layer of cells, while the central region, or cushion, is more massive ; and it is attached to the soil by numerous rhizoids. The whole is green and photosynthetic. In adult prothalli an acropetal succession of archegonia borne on the

lower face leads to the apex itself ; while the antheridia, which are commonly borne relatively early on the same prothallus, are scattered irregularly over the lower surface or margins of the basal region of the cushion, and on the lateral lobes. This being the commonest type of prothallus, it is often the only one mentioned in textbooks ; but variants from it are frequent even in

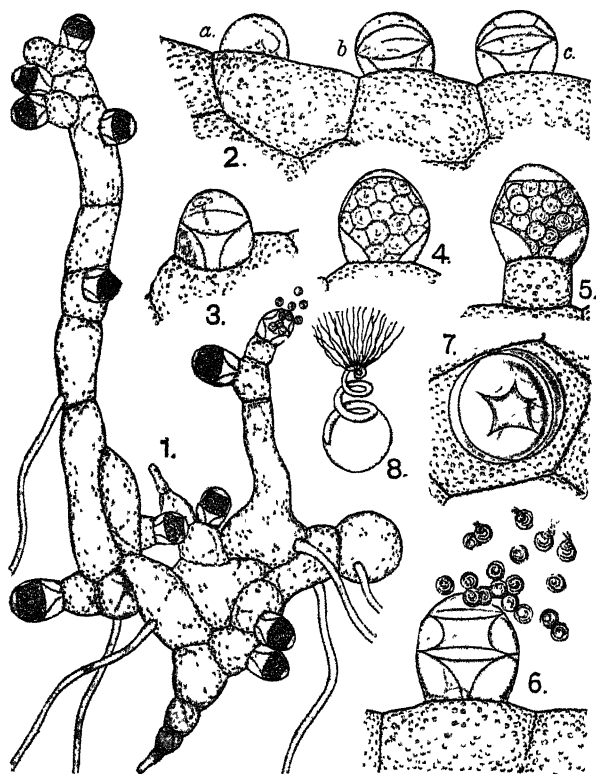


FIG. 365.

1. An attenuated male prothallus of *Nephrodium filix-mas* ; 2-5. stages of development of antheridia ; 6, 7. ruptured antheridia ; 8. a spermatozoid. (After Kny.)

Dryopteris itself, as well as in other Ferns. If the prothalli are crowded during development, and consequently starved, they assume a filamentous form with frequent branching, and bear antheridia only (Fig. 365). Prothalli of *Dryopteris* grown in deficient light may persist with attenuated form for years, bearing antheridia only. But if transferred to suitable conditions they will then develop normally and bear archegonia. Such facts suggest a plasticity comparable with that of the protonema and the Moss plant. In both cases the form of gametophyte appears to be more closely dependent on the conditions than that of the sporophyte. It is the same on germination of the spore, where insufficient light tends to prolong the usual filamentous stage.

On the other hand, occasionally in Polypodiaceous Ferns, and normally in the Marattiaceae, the filamentous stage may be omitted. In most cases it is only on some massive development of tissue that the archegonia are borne; but fertilisation of an archegonium habitually checks the growth of the prothallus that bears it. If, however, fertilisation of archegonia be prevented—for instance, by the absence of external water or by growth under deficient intensity of light for their formation—the prothallus may continue its development for five or six years: in such robust prothalli as those of Marattiaceae or Osmundaceae a length of two inches may be attained with occasional branching. They then resemble the fleshy thalli of *Anthoceros*, *Pellia* or *Aneura*. Such may be the variants of the ordinary cordate type. They show a high degree of plasticity in their relatively simple construction.

Commonly the apical growth arises from the distal end of the primary germinal filament, but this is not always so. For instance, in *Pteris longifolia* a spatula-shaped thallus is first formed; presently a meristem appears laterally, often with an initial cell, followed by one on the other side, when a lop-sided form is the result. A somewhat similar development leads to the formation of a perennating storage-tuber which burrows into the soil in *Anogramme*, and serves as an archegoniophore. This mode of perennation is after the model of *Phylloglossum* or of *Orchis*, though here the tuber is part of the gametophyte while in them it is the sporophyte that is so developed.

THE FILAMENTOUS TYPE

Certain Ferns are characterised by a more persistently filamentous thallus than those above described. This is seen specially in *Schizaea* and in *Trichomanes*. In the latter the filaments are green and transversely septate, and they are profusely branched: some of the branches develop as rhizoids. In

Schizaea fungal filaments are associated with these, as also sometimes happens in *Trichomanes*. The habit of the latter is shown in Fig. 366, together with a

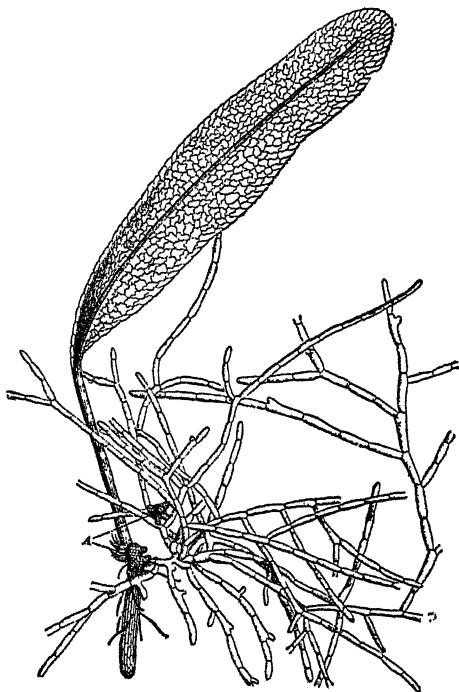


FIG. 366.

Trichomanes rigidum. Prothallus of filamentous type, with archegoniophores (A), on one of which an embryo plant is seated. × about 50. (After Von Goebel.)

young sporophyte plant produced from one of the archegoniophores (*A*). These prothalli may be multiplied by vegetative gemmae, which are borne distally, after the manner of certain Bryophytes; and they germinate on separation to produce fresh filamentous prothalli. In some species of *Trichomanes* the branches widen out into broadly flattened expanses one layer of cells in thickness, but they never seem to take the cordate form. They resemble the thin strap-shaped prothalli of the related genus *Hymenophyllum*, or those flattened protonemal expanses described for *Sphagnum* and *Tetraphis* (Chapter VI). The very irregularly branched prothalli of *Vittaria*, which are only one layer of cells in thickness, and bear gemmae, may also be compared with these. They do not take the cordate form with a single growing point, but possess marginal growth which produces numerous marginal lobes. These somewhat similar forms of prothallus are seen in Ferns not closely allied to one another in the characters of the sporophyte, and therefore they cannot be held as phyletically related to one another. But they have a common habit, for they are all epiphytic except *Schizaea*, which is a ground dweller, usually found among *Sphagnum*. The circumstances of epiphytic growth may perhaps favour such development as they show, together with the vegetative propagation by gemmae.

THE MYCORRHIZIC TYPE

A third type of prothallus, seen in the Ophioglossaceae, is colourless and develops underground: it is saprophytic, with mycorrhizic nutrition. Its habit is shown in Fig. 367, for *Helminthostachys*, which was investigated by Lang. A massive prothallus has also been described for *Ophioglossum vulgatum* (Fig. 379, p. 450), and for *Botrychium Lunaria* by Bruchmann: and for *B. virginianum* by Jeffrey. The form may vary, but the essential features are the same for all three genera, being fleshy and cylindrical, or in *Botrychium* slightly flattened. Occasionally the mycorrhizic prothallus may reach the surface of the soil, when it assumes a green colour, but does not develop further. In *Helminthostachys* the massive underground prothallus is erect, the lower part being irregularly lobed and hairy (*a, b*): this is the chief region of the mycorrhizic nutrition. It extends upwards into a cylinder free from fungus, and hairless, on which the gametangia are borne (*a, c*). In all the three genera the prothalli are homogamous, but in *Helminthostachys* there is a tendency to dioecism, the antheridia preceding the archegonia which are distal. The general analogy with the prothalli of the Lycopodiales is obvious (Chapter XIV); but certain important structural differences suggest that the similarity of form depends more upon sharing the same mode of life than upon real affinity. Comparison with other Filicales is more fruitful, and this is supported by a real similarity of the sexual organs to those of the Marattiaceae, though in these the prothallus is of the ordinary dorsiventral type

In certain Leptosporangiate Ferns it has been found that under special conditions of cultivation the flattened form of the thallus may be lost, the apex continuing its growth as a cylindrical process with structure, apical meristem, and disposition of the sexual organs as in the Ophioglossaceae (Fig. 368). The suggestion thus lies near to hand that if it were possible to cultivate

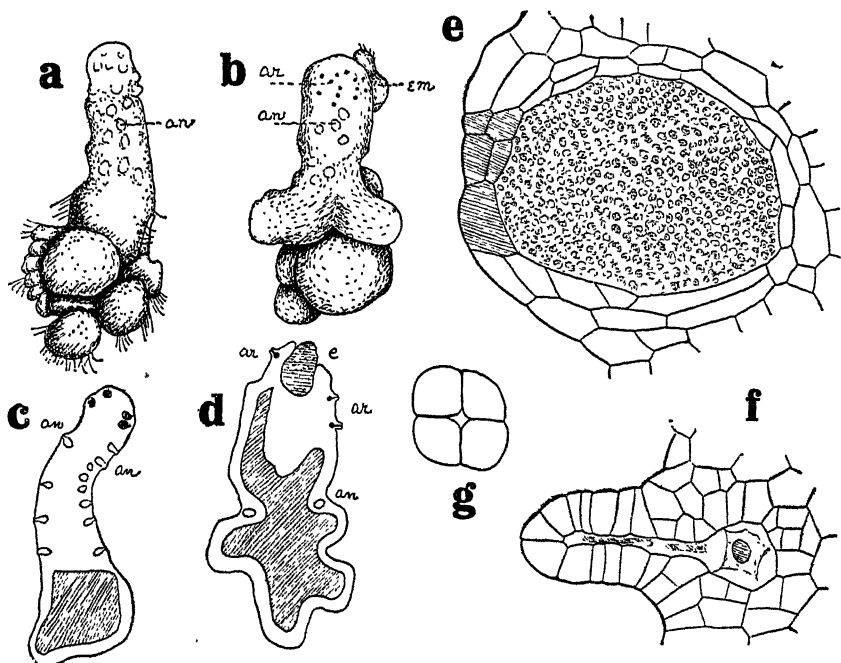


FIG. 367.

Prothallus of *Helminthostachys zeylanica*, as an example of the mycorrhizic type. *a, b*, adult prothalli seen from without; *c, d*, in section with the fungal regions shaded; *an*, antheridia; *ar*, archegonia; *em*, embryo; *e*, an antheridium; *f, g*, archegonium. (After Lang.) *a, b, c, d*, $\times 7$. *e, f*, $\times 200$.

ordinary fern-prothalli of a fleshy type, like those of the Marattiaceae, below the surface of the soil, a cylindrical form might be attained as in the Ophioglossaceae.¹ As bearing on this Campbell has found endophytic fungal

¹ See Lang, *Phil. Trans.*, vol. cxc., 1898, p. 187, etc. Also Land, *Bot. Gaz.*, 1923, p. 422. In describing the prothalli of *Angiopteris* collected on the Island of Tutuila, Land remarks that "perhaps the thallus of *Angiopteris* is well on the way to a subterranean habit. It is quite thick, and in many individuals the ventral sex-organ pad has become a more or less massive cylindrical structure. In some this cylindrical development has been carried so far that the wings of the thallus are inconspicuous, and some of the sex-organs are lateral and dorsal. . . . The thallus has also definitely acquired an endophytic intracellular fungus." He describes also the conditions under which they grew, thus: "The friable soil was continually falling, and burying the prothallia, some of which, though completely buried, were still vigorous, and bore sporelings. This condition is very suggestive of the way in which the subterranean habit of the gametophytes of some Lycopodiaceae and the Ophioglossaceae may have originated."

filaments in the central region of the prothalli of all the genera of Marattiaceae. Such facts may point to either of two lines of interpretation : they might suggest that the cylindrical form was relatively primitive, and the cordate type a derivative state consequent on emergence to a photosynthetic life at the surface ; or that a fleshy habit, and perhaps a cylindrical form with photosynthetic nourishment, was primitive, and that where mycorrhizic nutrition existed this made the saprophytic underground habit possible ; while, on the other hand, where photosynthetic nutrition predominates, the development might be either towards a flattened green expanse, as in the

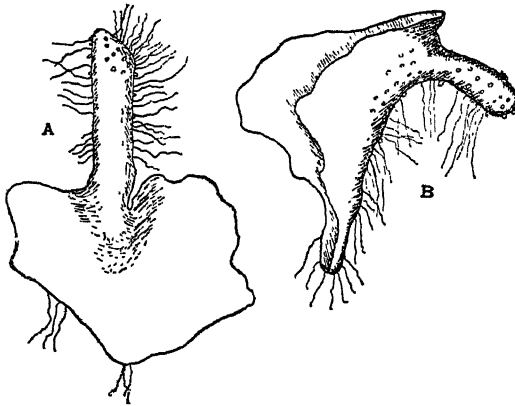


FIG. 368.

Prothalli of *Scolopendrium*, after Lang. They have grown out, when unfertilised, into "cylindrical processes," arising (A) from the apex, (B) from the under surface of the prothallus, and they bear sexual organs all round. $\times 6$.

cordate type : or, again, it might be attenuated and branched, under special biological conditions such as epiphytism, as is seen in the filamentous type. In support of a fleshy habit as primitive, whether cylindrical in form or not, there is the important fact that in both of the archaic families of living Ferns, viz., the Ophioglossaceae and the Marattiaceae, the gametangia are themselves massive and sunk in the tissue of the thallus.

It must be realised that this short statement draws attention only to the most outstanding variants of prothallial form in Ferns. It will, however, suffice to show that the usual cordate type is only one among several, and not itself necessarily the most primitive form of prothallus in Ferns.

THE GAMETANGIA

In contrast to the plasticity of the prothallus itself stands the high degree of standardisation of the gametangia of Ferns, and particularly of the archegonia. Those typical of the Leptosporangiate Ferns are described in all elementary books, and illustrated by means of certain familiar examples

(Figs. 364-5). It may be well here to cite the antheridia and archegonia of some less familiar types. In *Woodsia ilvensis* the antheridium originates from a single projecting superficial cell which, after successive cleavages, has the structure of a single central mother-cell of the spermatozooids: it is enclosed by a wall one layer of cells in thickness, derived from two successive ring-like tiers with a distal operculum (Fig. 369). There may be differences in the number and position of the first and subsequent segmentations that form the wall, but in Leptosporangiate Ferns it always consists of a single layer of cells only. The number of subdivisions of the internal mother-cell may also vary: each spermatocyte forms one spermatozoid. A common number of

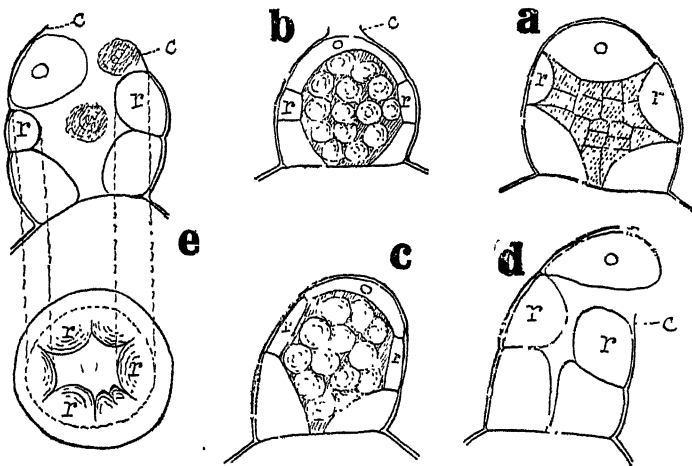


FIG. 369.
Antheridia of *Woodsia ilvensis*, after Schlumberger. *a*=antheridium with spermatozytes; *b*=ripe antheridium with cuticle ruptured; *c*, *d*=same antheridium before and after dehiscence; *e*=lateral and vertical aspects of ruptured antheridium. *c*=cuticle; *o*=opercular cell; *r*=ring-cells.

them is about 32, but it may rise to 100 or more. In *Woodsia* the number of spermatozytes seen in section is about 16, but the total in each antheridium is naturally much larger (Fig. 369, *a*). Rupture is caused by mucilaginous swelling of their walls, leading to pressure upon and tearing of the cuticle; the distal opercular cell (*o*) separates as a whole, and is extruded; the adjoining cells of the wall then become distended inwards, thrusting out the contents (Fig. 369, *b*, *c*). Von Goebel states that rupture in all Leptosporangiate Ferns is by bodily extrusion of the distal opercular-cell, not by irregular tearing of its walls. Though there may be differences in size, and particularly in the number of the spermatozytes in each, the type of structure of the projecting antheridium shows high constancy in the Leptosporangiate Ferns.

But the antheridia of the Eusporangiate differ widely in size from those of the Leptosporangiate type. They are more massive, and are deeply sunk

in the tissue of the prothallus. The very numerous spermatocytes which they contain are covered in by a wall of which certain cells may divide periclinally ; but one at least remains undivided, and may act as an opercular cell ; or there may be several of them, as in *Botrychium*. A layer of slab-like cells cut off from the adjoining tissue of the prothallus sometimes surrounds the mass of spermatocytes, and is nutritive in function, like a tapetum. Later

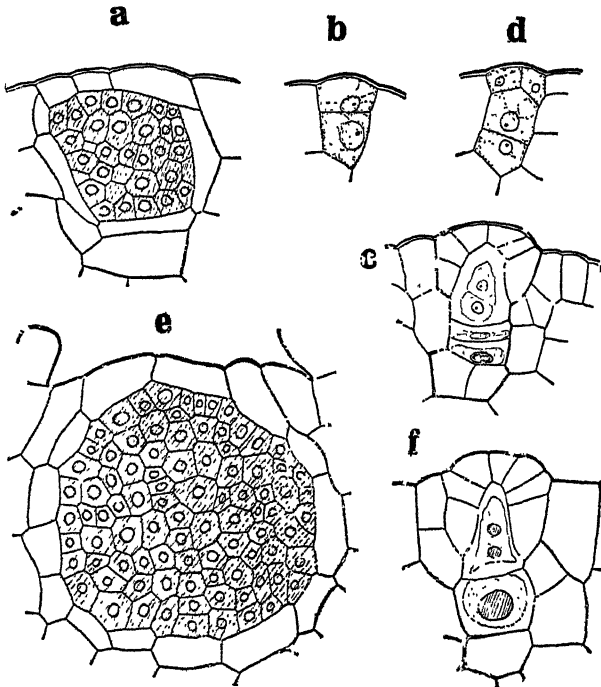


FIG. 370.

a-d = *Marattia Douglassii*, after Campbell; *e-f* = *Ophioglossum pendulum*, after Lang. *a* = antheridium with divisions of spermatocytes (32) in section, perhaps not complete; *b* = young antheridium; *c* = archegonium of *Marattia*. *d* = young archegonium; *e* = antheridium with 88 spermatocytes in section; *f* = archegonium of *Ophioglossum*.

these cells assist in the extrusion of the spermatocytes by swelling into the antheridial cavity (Fig. 370, *a*, *e*).

A comparison may be drawn between the Eusporangiate and the Leptosporangiate Ferns in respect of their antheridia and their sporangia, as taken from the gametophyte or the sporophyte of the same species. These organs are essentially different, and occupy distinct places in the life-cycle ; but both are conservative in their characters, and so serve to accentuate the difference between the ancient and the modern types. In both of these organs, whether antheridia or sporangia, there may be differences of position, relative to the surface that bears them : those of the Leptosporangiates projecting, while those of the Eusporangiates are partially or completely sunk. As to size a

rough and by no means exact numerical estimate may be made by counting the spermatocytes traversed in the median vertical section of an antheridium, and comparing it with the number of spore-mother-cells in a similar section from a corresponding sporangium. Such estimates are necessarily rough, and open to inaccuracy in detail ; notwithstanding such sources of error, the following table shows a substantial parallelism of the figures derived from well-accredited drawings, respectively for the spermatocytes and spore-mother-cells as seen in vertical sections of antheridia and sporangia of the Ferns named :—

NAME.	Sperma- tocytes.	Spore- mother- cells.
<i>Botrychium Lunaria</i> - -	130	220
<i>Christensenia</i> - - -	74, 60	74
<i>Angiopteris</i> - - -	55	67
<i>Gleichenia dichotoma</i> - -	42, 30	26, 25
<i>Dennstaedtia punctilobula</i> -	24	8
<i>Dryopteris filix-mas</i> - -	16	8 or less

Though these figures may be held as approximate rather than exact or stable, they point to a parallel progression of antheridia and sporangia in passing from the Eusporangiate to the Leptosporangiate types as regards the output of the propagative cells which they respectively produce. They indicate, perhaps more clearly than any other tabular statement has done, that progressive refinement of texture in the evolution of the Ferns which extends even to parts of distinct nature.

The archegonium is more highly standardised in Ferns as a whole than is the antheridium. Comparison may be made with a similar standardisation of the embryo-sac in Angiosperms. The uniformity of the archegonium has its biological foundation in the importance of sinking the ventral region, which contains the ovum, deeply into the protective tissue of the prothallus. The neck in Leptosporangiate Ferns projects with the well-known structure. Even *Osmunda*, which is archaic in so many features, shares this with the latter type (Fig. 371). But in Eusporangiate Ferns, such as *Ophioglossum* and *Marattia*, the neck itself is sunk almost to the level of the prothallial surface (Fig. 370, *e, f*). In all Ferns the segmentation is the same except for minor details. Each archegonium is derived from a single superficial prothallial cell : as in the antheridium this first divides by a periclinal wall, the inner cell dividing again, so that a series of three superimposed cells results. Of these the outermost forms the neck, dividing by crossed cleavages into a rosette of four cells : each of these by subsequent periclinal divisions, which vary in number in different Ferns, gives rise to one of the four rows which constitute the neck. The innermost, or basal cell takes no direct part in

further development. The middle cell of the series divides again periclinally to form the canal-cell and the central-cell. These each divide again periclinally. In the former the division is often incomplete, and confined to the

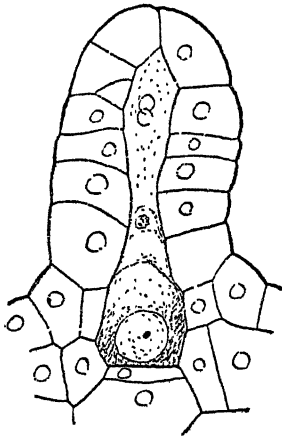


FIG. 371.
Mature archegonium of *Osmunda cinnamomea*. $\times 250$. (After Campbell.)

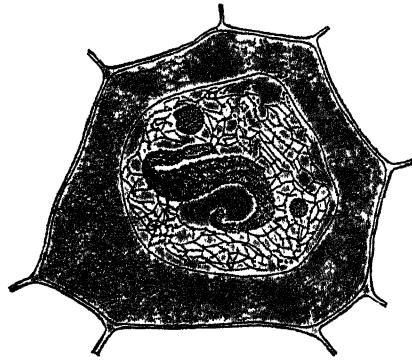


FIG. 371 bis.
Horizontal section of an egg of a Fern, showing a coiled spiral male nucleus within the female. Twelve hours. $\times 1200$. (After Shaw.)

nuclear division: in the central cell the last division gives origin to the ventral-canal-cell and to the ovum. A comparison of Fig. 370, *c, f*, with Fig. 371 shows a like result in all three, though the neck of the Eusporangiates is almost level with the surface of the thallus. These facts indicate the high degree of standardisation of the archegonium in Ferns.

THE EMBRYO

The act of syngamy consists in the fusion of spermatozoid and ovum, and the passage of the male nucleus into the female nucleus: their complete fusion follows (Fig. 371 *bis*). The roughly spherical zygote thus formed appears as a very uniform starting-point for the origin of the young sporophyte Ferns. The embryology of Leptosporangiate Ferns having been described in detail long ago, by many observers and in divers genera, and found to be strikingly uniform, the characteristic initial stages of their development were at first accepted as typical for the class, and used as a basis for wide-reaching comparisons with the embryology of other archegoniate plants. At one time there was even a tendency to read the features of all archegoniate embryos in terms of those of the Leptosporangiate Ferns. But the acquisition of additional facts, and the study of the biological conditions surrounding the nascent embryo, have tended to show that the Fern embryos first described are of a specialised type, and therefore ill fitted to form a basis for general comparison. With this *proviso* the embryogeny of Leptosporangiate

Ferns will be first described. It is given precedence in accordance with the early record of the details, rather than as a prototype.

The consequence of fertilisation *in situ* is encapsulation of the zygote, and it is followed by growth and segmentation. The first cleavage is by a

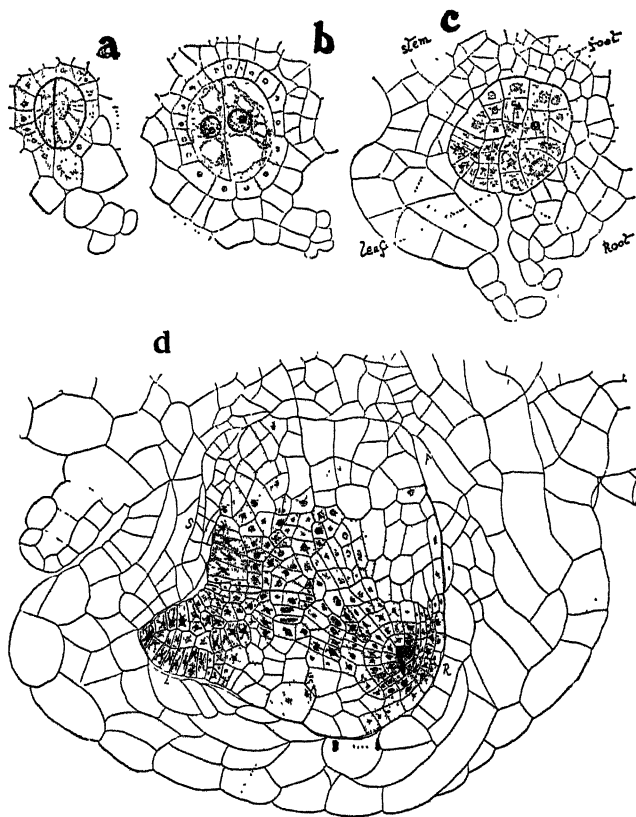


FIG. 372.

Young embryos of Ferns orientated with the archegonial neck downwards. The epibasal hemisphere is seen to the left, and the hypobasal to the right. *a*=two-celled embryo of *Adiantum concinnum* ($\times 30$ times scale); *b*=similar embryo of *Pteris serrulata* ($\times 30$ times scale); *c*=more advanced embryo of *A. concinnum*; the epibasal hemisphere has given rise to stem and leaf, and the hypobasal to root and foot. *d*=embryo of *Adiantum concinnum* more advanced, but still enclosed in the enlarged venter; showing character of the several parts. The orientation is as in *a*, *b*, *c*. S=stem; L=leaf; R=root; F=foot. (After Atkinson.)

basal wall, the plane of which includes the axis of the archegonium. Since this lies with its neck directed downwards, or obliquely acroscopic as regards the whole prothallus, the first wall is either vertical or slightly oblique to the direction of gravity. This basal wall separates an *epibasal* from a *hypobasal hemisphere*: the former is acroscopic, the latter basiscopic in relation to the prothallus which bears it. Each of these hemispheres then divides

into four approximately equal octants: the four constituting the epibasal hemisphere give rise to the axis and first leaf, the hypobasal hemisphere gives rise to the first root and the haustorial foot. The subsequent cleavages of the octants are of such a nature as to define respectively the apical cells of stem, leaf and root: the foot has no initial cell. The position of these parts,

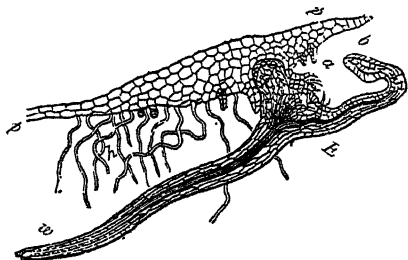


FIG. 373.

Adiantum capillus veneris. Longitudinal section through the prothallus, *pp*, and young plant, *E*. *h* = rhizoids of the prothallus; *a* = archegonia; *b* = the first leaf; *w* = the first root. $\times 10$. (After Sachs.)

and their relations to the archegonium and the thallus will be gathered from Fig. 372, *a, b, c, d*, which are all orientated approximately as in nature. The initial steps of embryogeny in the Leptosporangiate Ferns are very uniform, the stages of (*a*) and (*b*) leading to those shown in (*c*) and (*d*).

After the first segmentations are past a change of external form of the embryo becomes apparent.

The first leaf projects by its precocious growth from the lower epibasal quadrant, and it is followed by the first root which grows out from the adjoining hypobasal quadrant. Meanwhile the remaining epibasal quadrant, which gives rise to the stem, hangs back in its development, while the other hypobasal quadrant, together with some of the adjoining epibasal tissue, forms the foot, by which close physiological connection is maintained with the nutritive prothallus. Up to this point the embryo is still enclosed within the enlarging venter of the archegonium (Fig. 372, *d*).

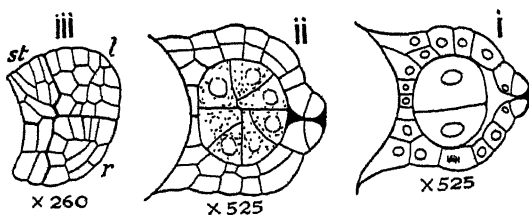


FIG. 374.

Embryos of *Marsilia vestita*, after Campbell. Orientated in their probable natural position, the megaspore normally lying flat on its side, with the archegonium distal in the apical prothallus.

But soon the leaf and root burst their way out: the former expands as the first nutritive leaf, the latter buries itself in the soil. Thus the embryo soon becomes self-dependent, and the prothallus rots away. It is then only a matter of time and opportunity for it to attain the characters of the adult (Fig. 373).

The embryology of the heterosporous Ferns gives further evidence of the stability of the early stages in the Leptosporangiate type. The megaspore

of *Marsilia* produces at its apex a minute prothallus, consisting only of a small number of cells, with a single archegonium. The megaspore being oval in form, it will usually lie with its axis horizontal, while that of the archegonium will be the same (Fig. 374). The first cleavage of the zygote is as before in the plane of the archegonium, but it is itself horizontal, the epibasal hemisphere being directed upwards and the hypobasal downwards. The octant segmentation and the origination of the stem, leaf, root, and foot bear approximately the same relations to the archegonium as in the homosporous types. The result, notwithstanding the minuteness of the prothallus, is a

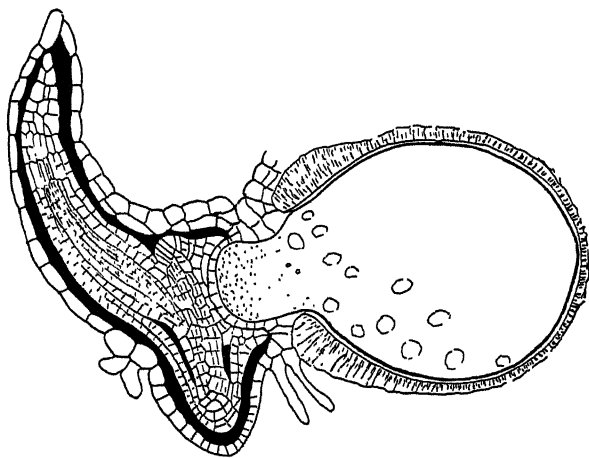


FIG. 375.

Median longitudinal section of a young sporophyte and megaspore of *Pilularia*, after Campbell, orientated as it would be in nature. $\times 70$.

sporeling comparable as regards the relations of its several parts to that of the ordinary Leptosporangiate type (Fig. 375).

The type of embryology thus described holds for all Leptosporangiate Ferns, subject to minor deviations in detail, such as the succession and exact position of cleavages. Even so important a primitive type as that of the Osmundaceae conforms to it in essentials, though not in detail. This is significant when considered in relation to the comparisons which have gone before (Chapters XVI.-XIX).

The best account of the embryo of the Osmundaceae is that given by Campbell.¹ The archegonium lies horizontally, projecting from the side of the midrib of the massive and fleshy prothallus. After fertilisation the first cleavage of the zygote is by a basal wall parallel to its axis; but the quadrant walls are also parallel with it instead of being transverse, although their position with reference to the axis of the prothallus is the same; so that the embryo-quadrants and the organs derived from them are situated like those of the Polypodiaceous embryo with reference to the prothallus, though not to

¹ *Mosses and Ferns*, 3rd edn., p. 356.

the archegonium. In the less regularity of its later divisions *Osmunda* appears to be intermediate between the Leptosporangiate and the Eusporangiate Ferns: moreover, the embryo retains for a longer time than in the former its globular form; the leaf also emerges later than in the Leptosporangiate Ferns, showing thereby a more primitive character. It is worthy of remark that the median plane of the embryo does not necessarily coincide with that of the prothallus.¹ The foot is large, and penetrates deeply, sometimes with superficial haustoria, as in *Anthoceros* or *Tmesipteris*. Thus the suggestions of primitive character are cumulative; nevertheless the embryo has the prone position, as against the erect habit of the Marattiaceae embryo.

It is in the Eusporangiate Ferns that the most interesting divergences of embryology are found from the simple type thus far described. In the Marattiaceae, as we have seen, the cordate prothallus is unusually fleshy, and the archegonia are directed downwards.

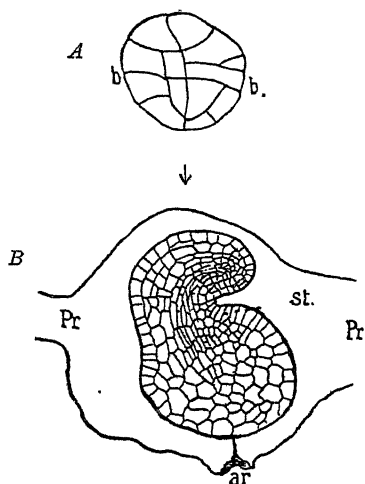


FIG. 376.

Marattia Douglasii. A=longitudinal section of a young embryo. $\times 225$. b, b =basal wall; the arrow points to the neck of the archegonium. B=a similar section of an older embryo, showing its position in the prothallus. *st*=stem; *Pr*=prothallus; *ar*=neck of archegonium. (After Campbell.) $\times 72$.

Here the basal cleavage of the embryo cuts the axis of the archegonium *transversely*: the polarity is thus vertical, and as the apex points upwards it is definitely *endoscopic*, in contrast to that of all Leptosporangiate Ferns, including *Osmunda*, where it is oblique. The result is that the upper surface of the prothallus, not the lower, is ruptured by the cotyledon, and the sporeling emerges with its apical bud erect (Fig. 376). This is found to be general for the family. If a series of embryos of the Marattiaceae be all orientated as they would be in nature they would appear as in Fig. 377, with the basal wall (b, b) approximately horizontal. The cleavages are less standardised than in Leptosporangiate Ferns, and the whole

development is more massive, while the differentiation of the parts, and particularly of the root, is delayed. In *Angiopteris* (*a*), *Christensenia* (*b*), and *Marattia* (*c*) there is no suspensor, and in this they conform to the usual type. But in certain species of *Danaea* (*d, e*) a short suspensor has been found. This goes with a pear-like form of the embryo, in contrast to the broadly elliptical form of other Marattiaceae. A suspensor has also been observed in *Macroglossum*: here the embryo is elongated obliquely, as though accommodating itself to the narrow bounds of the flattened prothallus. Nevertheless, the emergence of the shoot is by rupture of the upper surface, as in other

¹ Campbell, *l.c.*, Fig. 202.

Marattiaceae.¹ Lastly, though the embryo of *Angiopteris* has been repeatedly observed as conforming to the type of *Marattia*, Land has described how in

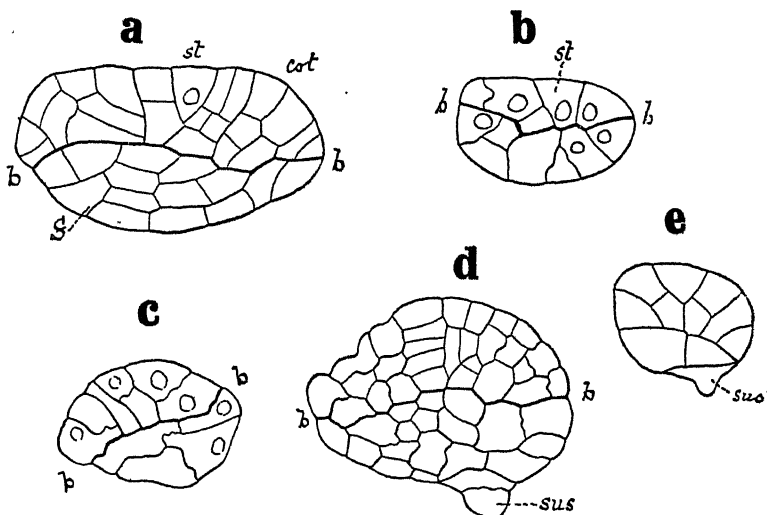


FIG. 377.

Embryos of Marattiaceae, all orientated with the archegonial neck downwards, as in nature. *a*=*Angiopteris*; *b*=*Christensema*; *c*=*Marattia*; *d*, *e*=*Danaea jamaicensis*. (All after Campbell.) *b*, *b*=basal wall; *sus*=suspensor; *st*=stem; *cot*=cotyledon; *f*=foot.

certain embryos of *Angiopteris* collected in the Island of Tutuila a suspensor is present, but not in all of them (Fig. 378). It is more elongated than in *Danaea*, and doubtless it has the effect of thrusting the embryo deep into the body of the nutritive tissue. It thus appears that in this very ancient family there is inconstancy in the presence of a suspensor, but constancy in the endoscopic orientation.

In the still more archaic Ophioglossaceae a like variability appears, certain types having a suspensor, others having none. Here also the latter were those first described, so they may be taken first. Bruchmann has shown how in *Ophioglossum vulgatum* the embryogeny is simple and direct, with no suspensor.² The cylindrical mycorrhizic

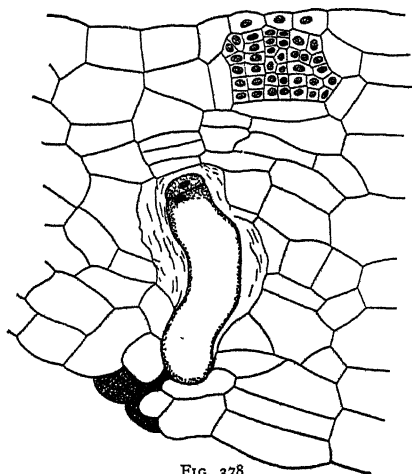


FIG. 378.

Section through a prothallus of *Angiopteris*. Above is an antheridium deeply sunk; below is a fertilised archegonium with an embryo showing a well-developed suspensor. $\times 200$. (After Land.)

¹ Campbell, *Ann. of Bot.*, Oct. 1914.

² *Bot. Zeit.*, 1904, p. 227.

prothallus bears numerous deeply sunken antheridia and archegonia intermixed; the embryo arises from one of the latter, the first external sign being

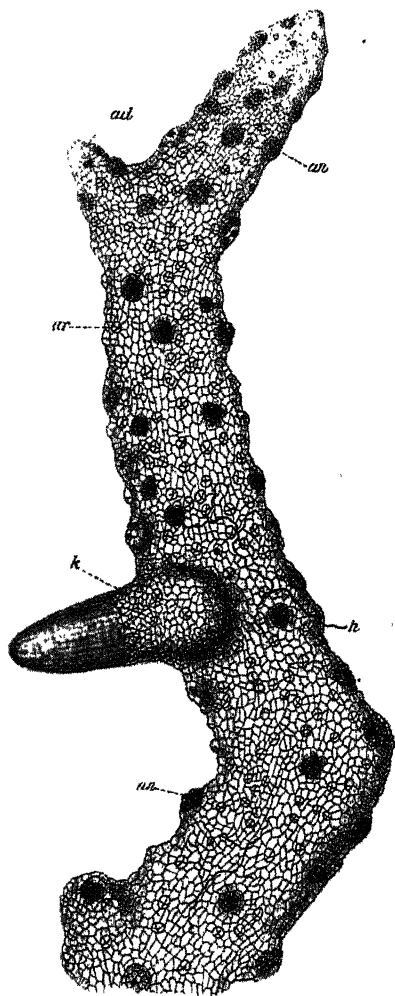


FIG. 379.

A prothallus of *Ophioglossum vulgatum* seen from without. $\times 30$. Numerous antheridia (*an*) and archegonia (*ar*) are present; *k* is a young sporophyte with a strong primary root; *ad* is an adventitious branch; *h*, the dark brown hyphae of a fungus, branches of which penetrate the prothallus. (After Bruchmann.)

the precocious mycorrhizic root; the shoot is delayed in its development (Fig. 379). This contrasts with the photosynthetic embryo of the Leptosporangiate Ferns, where it is the cotyledon that is precocious. The archegonium corresponds in essentials with that of the Marattiaceae, and the first cleavage of the zygote is transverse to its axis. But in contrast to these ferns the polarity of the embryo is exoscopic, the first wall separating an outer epibasal from an inner hypobasal hemisphere (Fig. 380). The relation of the several parts to the subsequent cleavages is obscured by their tardy differentiation. Bruchmann states that the hypobasal hemisphere provides the first root and foot, but the latter is never large. The root, however, rushes forward, defining its apical cell early (Fig. 380, *w*). It emerges from the prothallus before there is any definite trace of axis or cotyledon. Up to this stage the development may occupy several vegetative seasons. The development of the tardy shoot synchronises with the origin of the second root, which is endogenous, and the cotyledon lies on the same side as the first root (Fig. 381). But it

remains rudimentary, and is followed by a second leaf which develops above ground as a small sterile leaf. The third leaf may under favourable circum-

stances bear a fertile spike. The further development is as in the adult plant. As these parts advance the apex of the shoot hangs back, and becomes deeply sunk among the successive leaves with their basal sheaths (Fig. 381, s). These facts have their importance for comparison with the embryology of *O. moluccanum* and *pendulum*, as described by Campbell.¹

Bruchmann has also given a detailed description of the embryology of *Botrychium lunaria*, which, with certain differences of detail, corresponds to that of *Ophioglossum*²; while Jeffrey³ has published a full account for

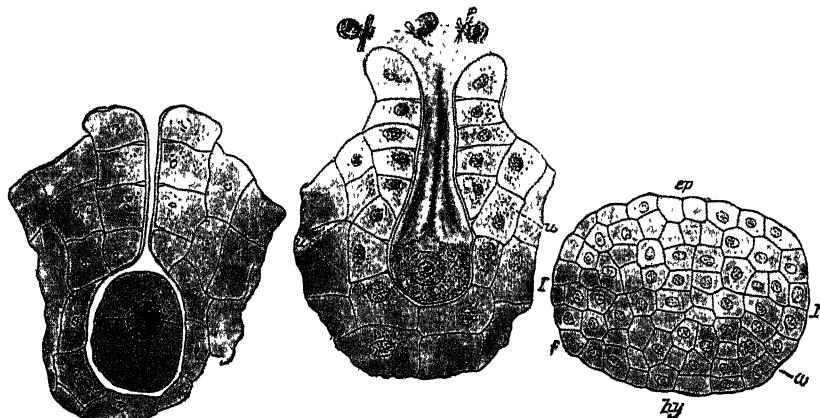


FIG. 380.

Ophioglossum vulgatum. The central figure shows an archegonium at the period of fertilisation. The left-hand figure shows the first division of the zygote. To the right is a more advanced embryo. *l*, *l*, the basal wall. *ep*, the epibasal, and *hy*, the hypobasal hemispheres. *f*=the region of the foot; *w*=the root. (After Bruchmann.) × 225.

B. virginianum. In all of these there is exoscopic orientation, and there is no suspensor.

These examples seemed to establish a direct type of embryology, without any suspensor, as representative of the Ophioglossaceae. But it has been shown first by Lyon in *Botrychium obliquum*,⁴ and later by Lang in *Helminthostachys*,⁵ that representatives of the family exist in which a suspensor is present, and the embryo undergoes curvature during its development. Moreover, in both of these the primary orientation is endoscopic. In *B. obliquum* the prothallus with its sexual organs resembles those of the genus, being tuberos, subterranean, and somewhat flattened, and the sexual organs being borne on the upper surface. After fertilisation the zygote elongates at first without division, penetrating deeply into the prothallus (Fig. 382). The

¹ See Chapter XXVI, on Embryology.

² *Flora*, 1906, p. 203.

³ *Trans. Can. Inst.*, 1896-7.

⁴ *Bot. Gaz.*, 1905, p. 203. See also *Land Flora*, p. 471, and Campbell, *Ann. of Bot.*, 1921, vol. xxxv., p. 140.

⁵ *Ann. of Bot.*, 1914, vol. xxviii., p. 19.

embryo is then segmented transversely from its tip, taking first a spherical form, and it divides with the usual basal wall; later the several parts differentiate as in other types of *Botrychium*, or as in *Danaea*. The epibasal hemisphere produces the stem-apex and cotyledon, while the root springs

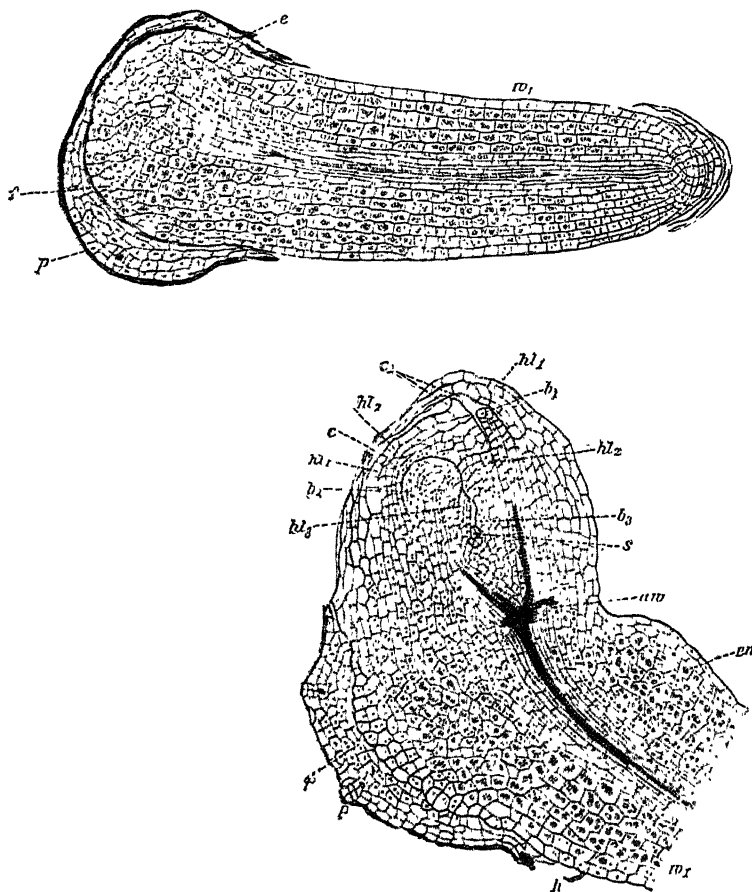


FIG. 381.

Ophioglossum vulgatum. The upper figure shows a young sporophyte in longitudinal section. *w*=first root with evident apical cell; *f*=the foot only slightly projecting; *e*=the epibasal region; *p*=the remains of the prothallus. The lower figure shows part of a large sporophyte in longitudinal section. *p*=prothallus; *w*=first root; *h*=an entering fungal hypha; *en*=endophytic fungus; *aw*=insertion of the second and third roots; *s*=apex of rhizome; *p₁, p₂, p₃*=leaves; *c*=canal; *hl hl*=sheaths of leaves. $\times 35$. (After Bruchmann.)

from the hypobasal, but very near to the basal wall. In the course of further development, since the axis of the archegonium is oblique, the embryo has to execute a more or less sharp curvature if it is to secure an upward direction for the shoot and a downward emergence for the root. This is a natural

consequence of the endoscopic orientation within the oblique archegonium. The curvature is carried out, and the final result is like that in the Marattiaceae, notwithstanding their downward-directed archegonia ; for in both the cotyledon ruptures the upper, and the root the lower surfaces of the flattened prothallus (Fig. 383).

Helminthostachys shares with *B. obliquum* the endoscopic embryology with a suspensor. Its roughly cylindrical, upward-directed prothallus is seen in Fig. 367, bearing archegonia with their axes approximately horizontal. The

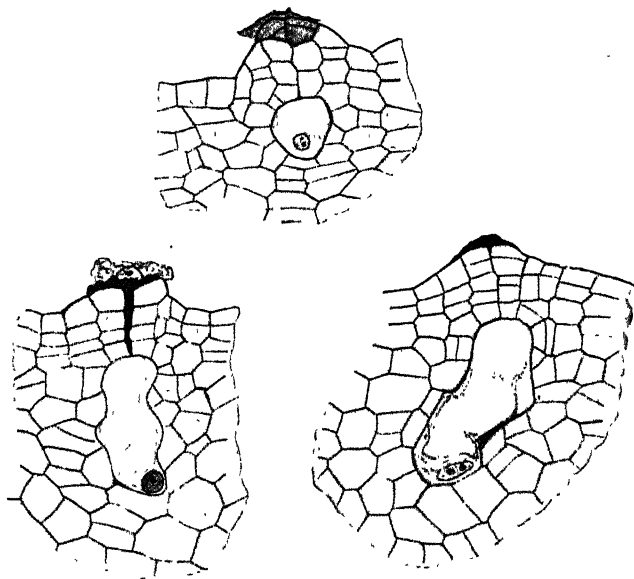


FIG. 382.

Botrychium obliquum. First stages in the embryogeny ; before the first segmentation the zygote grows into an elongated tube (the suspensor), which burrows its way irregularly into the tissue of the prothallus. $\times 150$. From sections lent by H. Lyon.

consequences of the endoscopic embryology and of the presence of a suspensor lead to a like curvature to that in *B. obliquum*, while the original relation of the parts of the embryo is essentially the same ; but here there is a proportionately larger foot (Fig. 384, *f*). This group of drawings represents three successive stages of the young sporeling of *Helminthostachys* : the suspensor (*s*, *s*₂) appears to be attached laterally, being displaced by the growth and curvature of the embryo. The three sporelings are orientated as they would be in nature, while the oldest (*c*) shows (on a smaller scale) the relation of the parts to the erect prothallus, and the fact that the first leaf emerges above ground as a photosynthetic organ. At first the axis of the sporeling in *Helminthostachys* is upright (*a*, *b*) : it is only as the plant passes to the adult state that its well-known creeping habit is assumed. This is the only member

of the family that takes this prone position, and it was probably acquired secondarily, in relation to its heavy foliage.

The embryos of the Ophioglossaceae thus present a very interesting problem of morphology. There are obvious analogies with the Marattiaceae, and also with the Lycopodiales. In all of these the problem is complicated by the presence of mycorrhizic nutrition, and by an underground saprophytic

habit. In all of them the orientation of the axis of the archegonium in relation to gravity is variable, while the suspensor is an inconstant feature. That problem will be discussed at length in Chapter XXVI, on the Embryology of Archegoniate Plants at large. Provisionally it may be stated here that a probable view, based upon the facts detailed above, is that the condition where a suspensor is present is archaic, and that by its elimination the embryo has solved an awkward problem of orientation. So long as the suspensor anchors the embryo in relation to the archegonial neck contortion of the sporeling would be necessary in order to secure an upright orientation of the shoot, except in certain favourable cases. Thus the state seen in *Ophioglossum* and in *Botrychium lunaria*



FIG. 383.

Botrychium (Sceptridium) obliquum, Muhl. Photo-micrograph of a section through a gametophyte and young sporophyte. The root is already protruded from the under side of the gametophyte. *a*=archegonium; *s*=suspensor; *t*=stem tip; *l*=first leaf; *r*=root. $\times 60$. (After H. L. Lyon.)

would be held to be a derivative state; and this would apply also to all of the Marattiaceae excepting *Danaea*, *Macroglossum*, and special instances of *Angiopteris*. It would also apply to all Leptosporangiate Ferns. In point of fact, a suspensor has been recorded only in those types of the Filicales which Palaeontology indicates as related to the Palaeozoic Flora.

The cumulative effect of the facts drawn from the prothalli and sexual organs of Ferns is to confirm on the one hand the essential unity of the Class of Filicales, and on the other to bring into a clearer light the relation between the Leptosporangiate and Eusporangiate types. That relation has so far been based on comparisons of form and structure, and of the propagative

organs of the sporophyte. But the gametophyte has been found so plastic, and at the same time so rudimentary in its vegetative outfit, that it can only serve as a secondary basis for comparison; in fact, so far as the sexual generation is concerned we are thrown back upon the gametangia. These leave no reason for doubt of the natural relation of all Ferns, *inter se*. But their details have a special value in the seriation of the Class. The tabulated numerical comparison of spermatocytes and spore-mother-cells in ancient and modern types given on p. 443 conveys more clearly than any other compact form of statement the validity of the general progress of construction in Ferns, from

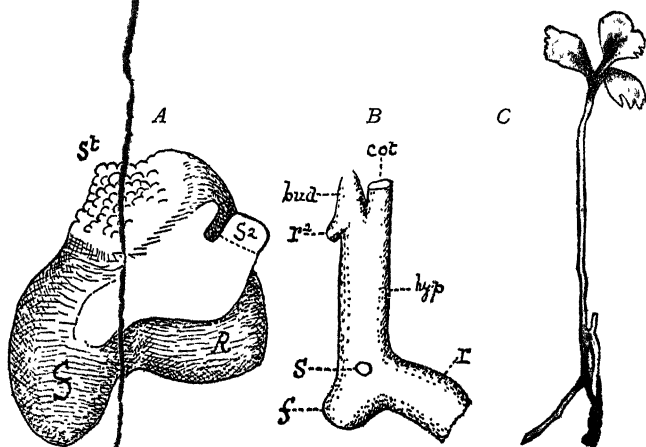


FIG. 384.

A, B, C=embryos of *Helminthostachys*. A shows a young state; B is more advanced; C is still older, with upright axis: it is natural size, while A and B are enlarged. f=foot. R, r and r₂=roots; st=stem; cot=cotyledon; hyp=hypocotyl; s, s₂=suspensor. (After Lang.)

the relatively massive Palaeozoic type to the more delicate type of the present day. It puts into figures a suggestion of that widely spread refining process, now demonstrated for the parts of both generations, which has characterised the evolutionary history of the Filicales.

Lastly, the embryology, though subject to inconstancy in the occurrence of a suspensor, demonstrates throughout the Class a high degree of constancy in the general character and relations of the parts. But in those types which are relatively massive, and are shown by comparison with the fossils to be archaic, the origin of those parts is not so early or so strictly defined in relation to the first cell-cleavages as in the later Leptosporangiate types. In fact, the embryology illustrates a progressive increase of precision in these first steps of organogeny; but there is no need to accord to that higher precision shown by the Leptosporangiate Ferns any greater morphological or comparative value than to the more massive and less precise organogeny of the Eusporangiate type.

CHAPTER XXII

A NATURAL GROUPING OF THE FILICALES¹

THE present work is not a systematic treatise ; it proceeds rather along lines of Comparative Morphology. Accordingly no detailed attempt will be made to range the several families of Ferns in any system of classification, but rather to indicate the salient steps which the Class appears to have taken in the course of its evolutionary history. The descriptions given in the preceding Chapters have shown that the Class is a very coherent and natural one ; though some of the Ferns, and in particular the Hydropterids, have run off into lines of high specialisation. But an examination of the details of their development leaves no doubt of their Filical character. It is true that the affinity of the Ophioglossaceae with true Ferns was in the past held as open to doubt. The view that they represent an independent phylum of the Ophioglossales was embodied in *The Origin of a Land Flora*.² But the last twenty-five years have yielded so many pertinent facts, and such suggestive new comparisons, that no doubt need be felt of the relation of that family with certain Palaeozoic Ferns ; and this notwithstanding that early fossil representatives of the family are wanting. On the other hand, the external organisation of certain other Fern-like fossils appears at first sight to relate these plants to the Filicales ; but, as the knowledge of their propagative organs has progressed, many of them have been proved to be seed-bearing plants, while their anatomical features also serve to distinguish them from true Ferns. They are now separated as the Class of the Pteridosperms.³ As regards their external morphology they provide one of the most remarkable examples of homoplastic likeness between distinct Classes. The result is that the Filicales, now including the Ophioglossaceae but excluding the Pteridosperms, stand as a coherent Class of which the better knowledge we now possess tends only to confirm the essential unity.

¹ This chapter contains a condensed epitome of the arguments and conclusions more fully stated in *Ferns*, vols. i.-iii. (1923-1928). In order to aid readers references are given to relative chapters of the more extended work. These were themselves based upon the "Studies in the Phylogeny of the Filicales," *Ann. of Bot.*, 1910-1923, where the detailed facts were still more fully presented ; and there also the relative literature is fully cited. Reference may also be made to the Hooker Memorial Lecture of June 1917, where "the Natural Classification of Plants" was discussed, with special reference to the post-evolutionary treatment of the Filicales. *Linn. Soc. Journal Botany*, vol. xliv., May 1918.

² Macmillan, 1908, pp. 463-494.

³ Scott, *Studies in Fossil Botany*, 3rd ed., part ii., 1923.

In the preceding Chapters a progressive refinement of constitution of the Ferns in the course of their evolutionary history has been shown as affecting all parts of their alternating generations. The demonstration of this is firmly founded on the facts of Palaeontology; indeed the relatively bulky Eusporangiatae may be accepted as representing the Palaeozoic type of the Class. Precedence will therefore be given to them: it is even doubtful whether any true Leptosporangiate Fern existed till Mesozoic time. Many Ferns of that period belong to families which exact comparison has shown to be intermediate in character, thus bridging the difference between the extremes and giving an evolutionary coherence to the whole Class.

The facts leading to the conclusion thus briefly stated have been worked out in much greater detail than has been here presented, in *Ferns*, vols. i.-iii.¹ The criteria of comparison, each of which is there submitted to detailed examination, are as follows: (1) external morphology of the shoot; (2) the initial constitution of the plant-body as indicated by segmentation; (3) the architecture and venation of the leaf; (4) the vascular system of the shoot; (5) the dermal appendages; (6) the position and structure of the sorus; (7) the indusial protections; (8) the characters of the sporangium and the form and markings of the spores; (9) the spore-output; (10) the morphology of the prothallus; (11) the position and structure of the sexual organs; and (12) the embryology of the sporophyte. Each of these topics has been touched upon in Chapters XVI to XXI of this work, and it has been found possible in respect of each to distinguish, with a high degree of probability, what was a relatively primitive state from that which has been relatively advanced in the evolutionary history. The archaic characters of the sporophyte, recognised as such by comparison of living and fossil Ferns, may be assembled into a verbal description, giving a composite picture of an archetype which should embody them all. Such an archetype would be based upon data actually observed, and not merely be an effort of imagination. If correctly drawn it may then be tested by comparison with the earliest fossil land-plants of which we have any detailed knowledge. It is believed that this method is more trustworthy than any general comparisons of land-plants with Algae: for comparison of Archegoniate with Archegoniate is closer than that of any Archegoniate with any Alga.

Such an *archetypic sporophyte* would have consisted of a simple upright shoot of radial symmetry, probably rootless, dichotomising if it branched at all, and with the distinction between leaf and axis either absent or ill-defined. The leaf, where recognisable as such, would have been long-stalked, with distal dichotomy, tending in advanced forms towards the sympodial development of a dichopodium. All the limbs of the dichotomy would be narrow and distinct from one another. The whole plant would be relatively robust as regards cellular construction, generally photosynthetic,

¹ Cambridge Press, 1923 to 1928.

and traversed by conducting strands with a solid xylem-core. The surface might be glabrous, or invested with simple enations. The solitary sporangia would be relatively large, and distal in position, with thick walls, and a simple method of dehiscence; and each would contain numerous homospores. Though the chief primitive features found in the sporophyte of Ferns are concentrated into this description it is not assumed that they will all be represented in the same individual or type, but it is quite conceivable that they should be.



FIG. 385.

Hornea Lignieri. Reconstruction, after Kidston and Lang.

It will be seen that this specification relates to the sporophyte only. The vegetative system of the gametophyte is so plastic that it does not yield stable comparative material. But the gametangia are more stabilised: the archegonium is so highly uniform that it again does not yield any wide field for comparison. But in Chapter XXI it has been shown by comparison of the antheridia with the sporangia of the same species that the features of these two quite distinct organs run substantially parallel, though the sporangia afford more reliable detail for systematic use. Accordingly, while the comparison of gametangia and sporangia has a high value, it is upon the features of the sporophyte that systematic comparison may best be founded.

The specification thus given is entirely based upon known Ferns, living or fossil. But if it be checked by reference to the form and structure of certain fossil types of the Devonian Period it is at once apparent that a real similarity exists between the verbal specification and plants which have actually

lived: for instance, *Hornea Lignieri* (Fig. 385). It is not suggested that the Psilophytales represent the direct ancestry of the Filicales. The intention is to indicate the general similarity which the verbal sketch bears to the most ancient land-living plants that are known in detail. The chief points of difference lie in the higher differentiation of the shoot shown by Ferns, and the presence of a root-system. But with the vegetative habit of the early Devonian Flora now reconstructed before us, combined with the proved similarity of primary vascular structure between axis and leaf in such fossils as *Botryopteris* and *Aneurophyton* (Kräusler), the origin of the axis and cladode megaphyll, by differentiation from an indifferent dichotomous system, emerges as a reasonably tenable hypothesis. On the other hand, the root-like rhizomes

of the Psilophytales and Psilotaes suggest a probable origin for true roots. Pending further discussion these suggestions point to a rational origin of the several parts of a simple Eusporangiate sporophyte from a type of less highly differentiated vegetation which existed early on land.

The Coenopteridaceae, including the Botryopterideae and Zygopterideae, which are known only as fossils, take their place as the characteristic Ferns of Palaeozoic time. Of these *Stauropteris* appears as a specially archaic type, with its upward-growing slightly bifacial rachis, and feathery assimilating branchlets, bearing isolated distal sporangia. Its anatomical structure suggests on the one hand the Psilophytales, on the other a Zygopterid character. No axis has yet been associated with these fronds; but the Zygopterids have a definite relation of axis and leaf, while their sporangia are associated in groups, suggesting lax uniseriate sori. Anatomically some of the Botryopterids indicate a primitively dichotomous relation of leaf and axis. The Coenopteridaceae may be fairly held to be Ferns, but themselves not highly standardised. They may be accepted as synthetic types representing, more than any others, such approximate sources as those from which the Class of the Filicales may have originated. In particular, that problematical plant *Stauropteris* gives a valid basis for comparison with the Devonian Psilophytales. Within the limits of variation in the last-named Class and in the Coenopteridaceae the essential categories of parts composing the sporophyte, viz., axis, leaf, root and sorus, may all be noted as in the making.

On the other hand, the Ophioglossaceae are without doubt the family of living Ferns most nearly resembling such early fossils as those just quoted. They appear as imperfectly modernised relics of an extinct Palaeozoic type; but they do not link on phyletically with any other living Ferns: in fact they stand rather isolated. But while the gametophytes of the Coenopterids are unknown, those of all three genera of the Ophioglossaceae are before us, and their embryology has been fully worked out; in this, as well as in the detail of the sporophyte, they afford a valuable basis for upward comparison. Both generations are of the type seen in Eusporangiate Ferns; it is true that in the structure of their apical meristems they take a middle position, but their sporangia all originate as massive growths, and their gametangia are sunken. *Helminthostachys* and *Botrychium* appear to be in many respects relatively primitive, while *Ophioglossum* may be held as specialised and derivative. *All the sporangia are distal or marginal, thus retaining what is regarded as a primitive position; and their spore output is large.* Significant features appear in the massive mycorrhizic prothallus, the sunken gametangia, and in the presence of a suspensor in *Helminthostachys*, and in certain species of *Botrychium*; while this organ is absent in other species, and particularly in *Ophioglossum*. The facts thus briefly summarised point collectively to a primitive state. The family has not been hitherto recognised among the fossils of the Primary Rocks. This regrettable fact may be due to their sappy texture.

A second living family of Eusporangiate Ferns of Palaeozoic type is that of the Marattiaceae, in which *the massive sporangia are grouped in superficial sori, a position that is regarded as secondary and derivative ; their spore-output is also large.* The position of the sori, which are often synangial, is related to the broadly expanded leaf-surfaces. Superficial synangia of like structure are present in the fossil *Ptychocarpus* from the Coal Measures, which shows that this Eusporangiate type dates back to Palaeozoic time (Fig. 301, Chap. XVIII). The Marattiaceae are again an isolated family, with no known living derivatives. Not only are the sporangia massive from the first, but the apical meristems also show complex segmentation. The sporophyte itself is large and its external form elaborate. Internally its vascular system is among the most complex known, and particularly that of the related fossil stems known as *Psaronius*. In certain types, and particularly in *Macroglossum* and *Danaea*, and occasionally in *Angiopteris*, a suspensor is present. The sum of these features accords with the fossil evidence in assigning a primitive position to the Marattiaceae.

A third Palaeozoic type of Ferns is seen in the Osmundaceae, which is a family well-represented to-day. They occupy an intermediate position in respect of many detailed features between the Eusporangiate and the Leptosporangiate Ferns. The spore-output per sporangium of 512 to 128 indicates this numerically. The type dates back to the Permian Period, and possibly to the Carboniferous, while recently tentative comparisons, already suggested long ago, have been strengthened by the recognition of the Permo-Carboniferous fossil *Grammatopteris* as a probable synthetic type, linking the Zygopterids with the Osmundaceae.¹ *Tubicaulis* from the Coal Measures may not improbably share this reference. There is no more interesting survival from the Palaeozoic Period than the Osmundaceae. The fossil story revealed by Kidston and Gwynne-Vaughan gives in illuminating sequence the steps of elaboration of the stele and leaf-trace within the family, as it passed on from the Permian Period to the present time. The living species take in their general organisation, in the primitive structure of their wood, and particularly in the detail of their sporangia and spore-output an intermediate place between the Eusporangiate and the Leptosporangiate types of organisation, linking the two together. This applies also to the gametophyte and the embryology.

At the moment, however, a feature that specially claims our attention is the way in which the living Osmundaceae link together two widely spread types of fructification in Ferns, viz., those with marginal and those with superficial sporangia. This distinction requires to be critically examined, so as to estimate its importance in the natural grouping of the advancing phalanx of Ferns. It has been seen that the two living families of Eusporangiate Ferns differ in the position of their sporangia. In the Ophioglossaceae

¹ Sahni, *Ann. of Bot.*, 1932, p. 863.

the parts which bear them are narrow, and often branched; and the sporangia themselves are distal or marginal, and often isolated. In the living Marattiaceae where the sporophylls or their segments are broad their position is superficial, and it is the same with the related Carboniferous fossil *Ptychocarpus*. It is a widely spread fact of experience among Ferns that where the fertile blade is expanded the sori are liable to leave the margin and to take a position on its surface. It is here that the two living genera of the Osmundaceae give valuable evidence. In *Osmunda* the fertile segments of the sporophyll are normally narrow, and the sporangia are borne in marginal tassels; but in the broader fertile segments of *Todea* the lax sori are superficial. Intermediate states may sometimes be seen in *Osmunda*, where on the widened and partially sterile segments the sporangia may be spread over the surface (Fig. 303).¹ If such facts stood alone a general conclusion might be drawn that the fertile segments are labile in this respect, and that the position of the sori and sporangia depended *directly* upon the degree of expansion of the leaf or segment that bears them. In some measure the Marattiaceae appear to support that view: for in the Coenopterid, *Corynepteris* (Fig. 296), the sorus is seated as a compact tassel at or near to the margin of a narrow leaf-segment, while in all the true Marattiaceae the sori, of similar or of elongated type, are clearly intra-marginal, and superficial. Comparison with *Corynepteris* would then suggest a ready adjustment of soral position to leaf-area similar to that seen in the Osmundaceae.

That the adjustment of soral position to leaf-expanse is not always so readily plastic as these ancient types appear to suggest, is shown by two other families of Ferns almost co-eval with the Osmundaceae, and again represented by many living species: viz., the Schizaeaceae, which are strictly marginal in the origin of their sporangia, and the Gleicheniaceae, which are as strictly superficial. These three ancient types probably represent as nearly as any others that are known the progenitors of modern Ferns. It is believed that they have severally remained distinct from Palaeozoic or early Mesozoic time, and that they and their derivatives represent phyletic lines that pursued their several courses apart throughout the intervening ages. Though the Schizaeaceae possess a very variable vegetative system, often with relatively primitive anatomy, they all agree in bearing solitary sporangia of strictly marginal origin. These may be shunted during individual development to a more or less superficial position on the lower

¹ Specimens of *Osmunda claytoniana* from Kashmir have been described by N. P. Chowdhury, *Journ. Ind. Bot. Soc.*, xi., 1932, p. 137. He draws from them, and by comparison with certain fossils, the conclusion that the superficial sorus was the primitive condition for the Osmundaceae. But all his facts appear to accord with those of Von Goebel: and with the view that (i) the original position of sporangia was distal or marginal, on a narrow base; (ii) that sporangia were liable to grouping as marginal tassels or sori; (iii) that these were liable to transition to the surface of a widening blade; and (iv) that Acrostichoid dissolution of sori may have occurred early.

surface ; but they all originate from marginal cells. These Ferns may be held as prototypes of such families as the Hymenophyllaceae, Dicksoniaceae, Davalliaceae, and finally of the Pteroid Ferns, in all of which a marginal origin of the sori is maintained, or at least indicated. They together constitute the great sequence styled the *Marginales*. On the other hand the Gleicheniaceae have a very uniform and characteristic vegetative system, with primitive anatomy. The sorus is of the radiate type, and it originates uniformly by outgrowth from the surface of the leaf or segment. These Ferns prefigured such later types as the Matonineae, Cyatheaceae, and the Dryopteroid and Asplenoid Ferns, and many others. All of these have in common an origin of the sorus from the lower surface of the leaf or segment, and they may be designated collectively the *Superficiales*. The Schizaeaceous type dates through *Senftenbergia* and *Klukia*, certainly from a Jurassic and probably from a Carboniferous source. Throughout the intervening ages the primitive marginal position of their sporangia and sori appears to have been maintained by them, and by their derivatives. Similarly the Gleicheniaceae type finds its correlative in the Carboniferous fossil *Oligocarpia*, and their superficial sori may be followed onwards to the present day. It is true that the ancient Osmundaceae suggest even in the living types a ready transition from the marginal to a superficial position, and that among the *Marginales* a frequent demonstration has been given of the "phyletic slide" of the sorus from the margin to the surface. It is particularly evident in the Davallioid and Pteroid Ferns that such a passage from the marginal to a superficial position has happened, and even repeatedly throughout the course of evolution. Such facts may seem to detract from the value of this distinction of soral position. *Its real value lies in the early or late date of the event of transition from margin to surface.*

This discussion may be summed up as follows. Wide comparison shows that the original position for all sporangia was distal, or as the cladode became flattened, marginal. That the marginal position has been pertinaciously held by certain Ferns from Palaeozoic times, and even to the present day. These are typified by the Schizaeaceae. Those which assumed the superficial sorus in Palaeozoic times, and have as persistently retained it from then till the present day, are typified by the Gleicheniaceae. It is believed that these two great sequences have been distinct from one another phyletically since Palaeozoic times, and this is the ground for their being segregated, together with their derivatives, under the names respectively of the *Marginales* and the *Superficiales*.

Lastly, there is a series of Ferns with their sporangia loosely disposed on the lower surface, after the fashion of *Todea*. There is little or no evidence of their having ever possessed definite sori, or any organised indusial coverings. These are the Gymnogrammoid Ferns. They do not readily link on either with the *Marginales* or the *Superficiales*, and they may have originated

through a type such as the isolated *Plagiogyria*, from an Osmundaceous source, as it is seen in *Todea*. This description will be aided and elucidated by the subjoined scheme, which is designed to convey the relations of the more prominent groups of Ferns, as based upon general primitive character on the one hand, and on relation of sori to the leaf-margin on the other.¹ The scheme visualises the conclusions above stated without unduly crystallising them : for the lines are left disconnected, so as to avoid any idea of direct

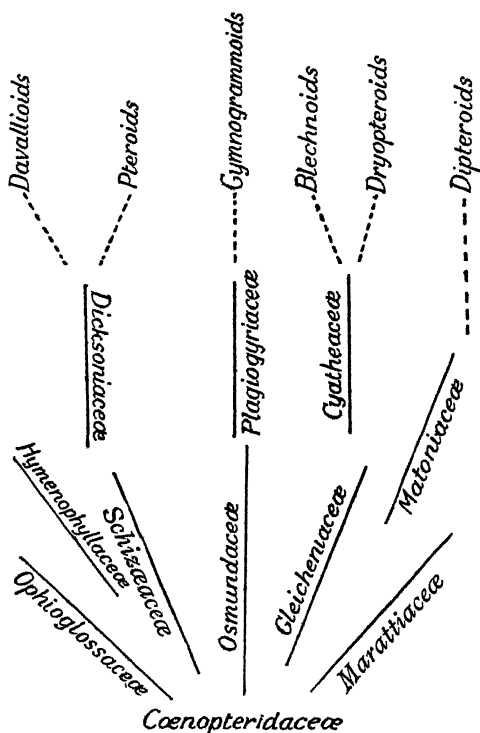


Fig. 386

descent, while conveying some approximate suggestion of probable relations. The marginal types are placed to the left, and the superficial types to the right. The Simplicies take their place below, where the Palaeozoic types are naturally to be found ; while the Mesozoic types, many of them being gradate, are ranged above them. This is the length to which the above paragraphs will have led. Five chief families of the Simplicies are represented as radiating from the Coenopteridaceae, the Osmundaceae taking a central place between the marginal and the superficial types. Three or perhaps four derivative lines may be traced from these, the most important being the marginal

¹ *Ferns*, vol. ii., chap. xxxi.

Dicksoniaceae, here associated with the marginal Schizaeaceae, from which (together with the Hymenophyllaceae and Loxsomaceae) they were probably derived ; and the superficial Cyatheaceae related to the superficial Gleicheniaceae. The Osmundaceae have commonly been thought to have had no direct descendants, and this may still be true. Nevertheless, the curiously isolated little family of the Plagiogyriaceae, represented only by the genus *Plagiogyria*, finds its probable affinity in wide comparison with *Todea* : and it is so placed in the scheme.¹ On the other hand, there is the ancient genus *Matonia*, which is in respect of its sorus one of the Simplices. Its relation to the Gleicheniaceae is undeniable.² But its nearest affinity is with the genus *Dipteris*, both being living representatives of a type widely spread and prevalent in the Mesozoic Period. As to soral conditions, the Dicksoniaceae and Cyatheaceae have gradate sori, while *Matonia* retains the simple sorus of the Gleichenioid type. The lax sorus of *Plagiogyria* is of the type of *Todea*, but with a tendency toward the "mixed" state. There are thus indications of soral advance, and of the intermediate character of these Ferns between the ancient Simplices and the Mixtae. This accords with the place assigned to them in the scheme on grounds of general comparison.

Of the relatively primitive families there remain the Hymenophyllaceae and Loxsomaceae, the relation of which to the Schizaeaceae is suggested by the place assigned to them in the scheme. A Jurassic fossil, *Stachypteris*, proves the early existence of a marginal and probably gradate sorus such as they possess ; but early fossil records of these families are doubtful. The Hymenophyllaceae are the well-known "filmy Ferns," strongly represented and widely spread in the current Flora. By comparison their place is in general correspondence with the Schizaeaceae and Dicksoniaceae ; but the Loxsomaceae are the nearer to the latter family.

Looking upwards to the great mass of the Leptosporangiate Ferns, which with their various forms, so rich in genera and species, constitute the Fern-Flora of the present day, they show a "mixed" character of the sorus as prevalent over the earlier simple state. The intimate relations of the modern families of Ferns have greatly taxed the insight of systematists ; but it has been found possible, by comparison based upon all the twelve criteria above enumerated, to segregate them into six chief lines, or phyla, and to relate these to the primitive types included in the lower part of the scheme. Naturally these phyla may be themselves further segregated as the basis of comparison is extended so as to test the provisional conclusions of the systematists. Here it must suffice to indicate that each of the phyla centres round some well-known generic type : and to give a very brief sketch of each, leaving more detailed analysis to special systematic works.

The derivative phyla related to the Dicksoniaceae are the Davallioid and Pteroid Ferns. Systematically these have usually been treated apart, but

¹ *Ferns*, vol. ii., chap. xxxi.

² *Ferns*, vol. ii., chap. xxv.

they possess many features in common. The Dennstaedtiinae rather than the Dicksonieae themselves offer suggestive lines of connection: and in particular the series *Cibotium*, *Dennstaedtia*, *Hypolepis* provides an example of phyletic advance towards the superficial mixed sorus found in most of the Davallioid and Pteroid Ferns.¹ The Davallioid Ferns centre round *Davallia*, a genus well represented in ordinary cultivation. The Pteroid Ferns centre round the Bracken (*Pteridium*) (Fig. 322), which leads on to the genus *Pteris* itself. The chief diagnostic feature is that in the former the sori are usually, though not always, separate and marginal, with a double indusium: but in the Pteroid Ferns the originally marginal sori merge into linear sequences, and tend to spread on to or even over the whole of the lower surface, while the lower indusium becomes vestigial or even abortive. Intermediate steps show how these states were attained.

The *Davallioid Ferns* include some ten genera, and about 200 species, for the most part with a creeping habit and variously divided leaves.² The vascular system is often complex. Dermal appendages appear as scales. The sorus is originally a two-lipped one, as it is in the Dennstaedtiinae; but it tends to pass from a marginal to a superficial position, with the margins of the lower indusium adherent to the surface of the blade, so as to form a sort of pocket. The upper indusium meanwhile becomes merged with the upper surface, as in *Hypolepis*, and other Ferns (Fig. 307). The result is that the sorus often appears to be intra-marginal. The receptacle becomes flattened in relation to the mixed condition of the massed sporangia, which are themselves long-stalked, with a vertical annulus. All of these are features of advance as compared with the Dicksonioid type. The sori of *Davallia* as a rule maintain their identity, but in *Lindsaya*, *Diellia*, and *Nephrolepis* coenosori, with a vascular commissure, become a more or less marked feature. This formation of coenosori appears to be phyletically independent of that in the Pteroid Ferns.

The *Pteroid Ferns*³ include some six genera, and about 200 species. A central type would be of rhizomatous habit, with pinnate leaves and open venation, and with marginal coenosori resulting from lateral fusion: they thus form a continuous receptacle, with a vascular commissure traversing it. These general characters appear in *Pteridium*, the Common Bracken (Fig. 322). Notwithstanding the very complex anatomy of the Bracken this single cosmopolitan species proves to be the most primitive of all Pteroids. Among other features it bears hairs only, but dermal scales are present in the more specialised types. The primitive character appears particularly in the structure of its strictly marginal, two-lipped coenosori, which in certain varieties present a persistent basipetal sequence of the sporangia, on a still conical though lop-sided receptacle. These soral features, together with the

¹ See *Ferns*, vol. ii., chap. xxx., and vol. iii., chap. xxxvi.

² *Ibid.*, vol. iii., chap. xxxvii.

³ *Ibid.*, vol. iii., chap. xxxviii.

dermal hairs, correspond to those of the Dicksoniaceae. But in *Pteris* itself the sorus has slid to a superficial position, and the lower indusium is aborted, while the upper is merged in the leaf-surface. The receptacle in *Pteris* is flattened, and there is no clear indication of a basipetal sequence of the sporangia. In some species of *Pteris*, however, the flattened receptacle becomes widened so as to cover a broadening band of the leaf-margin. Finally, in the three species of *Acrostichum* a successively increasing spread of the receptacle encroaches further over the surface, till in *A. aureum*, the common inter-tropical swamp Fern, the whole lower leaf-surface appears fertile. This Acrostichoid development may be held as an extreme advance from the original Dicksonioid source (Fig. 325).

Here the romantic story of the genus *Acrostichum* may be briefly told, for it has a didactic value. The genus was founded by Linnaeus in 1753 upon the Fern still known as *Acrostichum aureum*. The extended fertile area was taken as the leading generic character. All Ferns having their fertile leaf-area similarly extended were at first designated "Acrostichum," and included in the genus irrespective of habit or of detailed structure. The genus grew to unwieldy proportions, till in the *Synopsis Filicum* of 1883 it included 132 species, with various ill-coordinated Sections. But gradually a perception of natural affinities led to the breaking up of the incoherent group. It was perceived that the spread of the fertile area over the leaf-surface can happen in various affinities, and groups of "Acrostichoid" species were successively detached from the genus, and ranked with their congeners of similar general character. Thus the unwieldy genus was gradually whittled away, till now the only remaining representatives of *Acrostichum* are the original type, *A. aureum*, and a couple of related species. The last step has been to show that from general comparison, and particularly from the vascular anatomy, *Acrostichum* is really a Pteroid Fern in which the coenosorus has widened and spread more or less completely over the lower surface. Thus, at last, the original type of *Acrostichum* has come into its own. After the lapse of nearly two centuries, including a period of great systematic confusion, the generic designation is upheld in its original purity. But the type is now demonstrated as an extreme derivative of the Pteroid alliance, and its probable ultimate source lies among the Dicksonioid Ferns.

The moral of this story is, not to make a single character the foundation of a genus: least of all one that is likely to result from polyphyletic advance. But in drawing a generic diagnosis the net should be cast as widely as possible over the area of observed fact. This is the true spirit of a natural classification.

The *Gymnogrammoid Ferns*¹ centre round the old genus *Gymnogramme*, in which the superficial sori are more or less extended along the veins without any specialised indusium. As presented in Hooker's *Synopsis Filicum*, and by Diels in the *Natürl. Pflanzenfam.* of 1902, they are associated with the Pterideae. But the mere absence of an indusium may have resulted either from abortion, as in the lower indusium of the advanced Pteroids; or there

¹ *Ferns*, vol. iii., chap. xxxix.; also vol. ii., chaps. xxi., xxii., xxxi.

may never have been an indusium at all in the phyletic history. The first question will then be whether there is in the Gymnogrammoids any vestigial evidence of an indusium, and in particular of a lower indusium. No such evidence is forthcoming in the Ferns here ranked as Gymnogrammoid. It is therefore necessary to consider what other types of non-indusiate Ferns of primitive type exist, in relation to which the origin of the Gymnogrammoids may be traced. Such are found in the genera *Todea* and *Plagiogyria*, while the Schizaeaceae may also be borne in mind, particularly *Mohria* and *Anemia*. Such relations are suggested by the place assigned in the scheme to the Gymnogrammoid Ferns.

These Ferns may be grouped in four sections: first, those showing a relatively primitive state, such as *Cryptogramme* and *Llavea*; secondly, the genera which are naturally grouped round *Gymnogramme* itself; thirdly, the large and specialised genus *Adiantum*: and, lastly, the specialised xerophytic types associated with *Cheilanthes*, *Pellaea*, and *Notholaena*. The first are probably most closely related to *Plagiogyria*, and ultimately to the Osmundaceae; the last have always been recognised as having features in common with the Schizaeaceae. Among these *Pellaea*, *Saffordia*, and *Trachypteris* are specially interesting as showing transitions towards an Acrostichoid state, which would naturally result from any spread of the unprotected sori from the veins that bear them to the general surface of the blade. The whole character of these Ferns seems to place them naturally between the marginal and the superficial series, as is the case with the primitive Osmundaceae with which a relationship may ultimately be traced.

The *Dryopteroid Ferns*¹ comprise the chief bulk of the advanced Superficiales: they may be traced back through some form of Cyatheoid affinity to an ultimate Gleichenioid origin, with superficial, typically radial, and simple sori. Such a sequence would have led from a non-indusiate source through an indusioid phase, and would terminate again in certain cases in a non-indusiate state. This would involve the origin, and in some cases the subsequent abortion, of an indusial covering. The sequence starts from a simple naked sorus of the type of *Gleichenia*. It is no great step, with *Lophosoria* as a link, to *Alsophila* with its naked but basipetal sorus (Fig. 315); in its congeners *Hemitelia* and *Cyathea* the "indusium inferum" becomes a marked feature, which probably originated from dermal hairs or scales. The closely related genera *Diacalpe* and *Peranema* indicate a probable relation between the Cyatheoids and Dryopteroids; in the latter the mixed and indusiate sorus became lop-sided in relation to the leaf-margin (Fig. 235). In some Ferns of this vast series the lop-sidedness became extended, giving the type of the Asplenioids; in others, by abortion of the indusium the sorus became naked, as in *Phegopteris*: or, again, by fusion of the naked sori and

¹ *Ferns*, vol. iii., chaps. xl., xli.; also vol. ii., chaps. xxiv., xxxii., xxxiii.

their spread over the leaf-surface the "Acrostichoid" state was acquired, as in *Polybotrya* and *Leptochilus* (Fig. 324). Some 2000 species are included in this very successful group, which includes a large proportion of the well-known Ferns of temperate climates. They are characterised by the great plasticity of their superficial, circumscribed, usually indusiate and mixed sori. The origin of their indusium appears to have been quite distinct from that of the Dicksonioid Ferns, being here referable to a fusion of hairs, or to a dermal scale (Fig. 316): and it is of most marked occurrence in forms which bear scales on their stems and leaves.

The following note is based on the above reference to *Phegopteris*. An extreme example of unnatural and unwieldy grouping of species in a single genus consequent on too loose a definition is seen in the Linnaean genus *Polypodium*. Nearly 400 species are assembled under that title in the *Synopsis Filicum*. The diagnosis as given in Hooker's *Species Filicum*, vol. iv., p. 163, stands thus: "Sori dorsal, usually sub-rotund, or more or less oblong. Involucre none. Veins free or variously anastomosing, with sori terminal or radial. Ferns of very varied form, size, and structure, etc." The process of disintegration of this incongruous crowd of species is already advanced, but not completed. A similar source of error underlies this old genus *Polypodium* to that already noted in the old conception of *Acrostichum*, viz., the adoption of too narrow a basis of diagnosis. From an evolutionary point of view the same end of soral character may have been derived historically, and therefore phyletically, along a plurality of channels. For instance, *Polypodium vulgare*, the Linnaean species of 1753, has probably been non-indusiate throughout descent, while abundant evidence shows that the species grouped under Presl's *Phegopteris* are really ex-indusiate Dryopteroids. On the other hand, comparative morphology and the fossil record combine to show that the species of *Dipteris*, still included under *Polypodium* in the *Synopsis Filicum* of 1883, represent a quite distinct though always non-indusiate phylum. These are mere examples chosen to illustrate the danger of a lax diagnosis, and the disintegrating effect of well-assured views of polyphyleticism.

The *Blechnoid Ferns*¹ include some eight genera, and about 200 species. They show a prevalent xerophytic character, with an erect or even dendroid, and alternatively a climbing habit; but the feature which is distinctive of *Blechnum* is that continuous coenosori run, one on either side of the midrib of the fertile pinna. The origin of this may be traced to those lines of separate sori in a like superficial position, seen in *Onoclea* or *Matteuccia* (Fig. 318). The soral fusion is similar to but phyletically distinct from that seen in the marginal Pteroids. Within the comprehensive genus *Blechnum* two types of fertile pinnae appear: that of *Lomaria*, where it has inrolled margins covering the coenosori, but it is not developed as a photosynthetic organ; and that of *Eu-Blechnum*, where the pinna, with coenosori protected as before, has become a photosynthetic organ, by the outgrowth of new photosynthetic flanges,

¹ *Ferns*, vol. iii., chaps. xliii., xliv.

one arising on either side from the regions of greatest curvature of the upper surface (Fig. 387). Alternatively, the coenosorus is liable to spread over the lower surface of the pinna, giving the "Acrostichoid" state, as seen in *Stenochlaena*, and *Brainea*. These peculiarities, together with the modifications of them resulting in the characteristic state of *Woodwardia*, *Doodya*, and *Phyllitis*, are described in *Ferns*, vol. iii., chapter xlv.

There still remain the *Dipteroid Ferns*,¹ a phylum the distinct position of which has not been sufficiently realised till recent times. The cognate types of *Matonia* and *Dipteris*, with their superficial and radiate sori, may be held as related by descent to the Gleicheniaceae stock. *Matonia* is technically one of the Simplices but with a distal umbrella-shaped indusium, which is

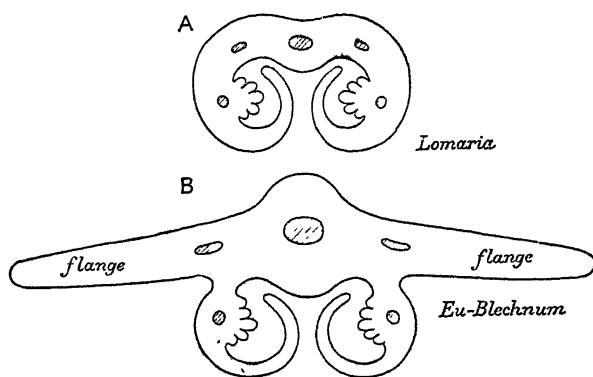


Fig. 387.

A = diagrammatic section of the fertile pinna of the type of *Lomaria*, with incurved margins, but no flange. B = a similar section of the type of *Eu-Blechnum*, showing the same parts as before but with the addition of flanges right and left. Compare Fig 317.

unique. *Dipteris* is non-indusiate, and in *D. conjugata* a "mixed" condition is seen in very simple form. This in more advanced development is characteristic of its derivatives, and in particular of *Cheiropleuria*. The Dipteroid derivatives are creeping or epiphytic Ferns, with dichotomously branching leaves, sympodially developed. Their venation is reticulate. In the original type the leaf-segments were narrow, with a row of isolated sori on either side of the midrib, as in *D. Lobbiana*. But with expansion and lateral webbing of the leaf as in *D. conjugata* the sori multiplied, and often in the derivative types the individual sori became extended and even fused, so as to give an Acrostichoid state. This is seen in *Cheiropleuria*, *Christopteris*, and *Platynerium*. It seems not improbable that other living genera, such as *Neochheiropteris* and *Pleopeltis*, are also related to this phylum. The spore-output is particularly interesting, for while *Dipteris* itself has a typical number of 64 spores per sporangium the living *Cheiropleuria* has 128; this

¹ *Ferns*, vol. iii., chap. xlv.; also vol. ii., chap. xxv.

finds its match in the Mesozoic Dipteroids, and numbers of 256 to 512 have been recorded for the fossil *Dictyophyllum*.

Ferns of this series have in the past been referred to affinity with various other families or genera, particularly with *Polypodium* and *Acrostichum*. It seems probable that they are now rightly recognised as forming a separate phylum of their own, which may be traced back to an early, perhaps Gleichenioid, source. The phylum appears to have retained its identity throughout Mesozoic time, and to have survived to the present day in such genera as those named. To their number additions may be expected as detailed knowledge increases.

This brief sketch of the phyletic grouping of the more advanced Leptosporangiate Ferns has only taken up the main lines. But sufficient evidence has been given of the complexity of the problem of the whole Class to prevent any presumption of finality in the results thus presented. There is no wonder that the pre-evolutionary systematists were often misled by apparent similarity of the propagative organs of the sporophyte, upon which their classifications were mainly based. Consequently they often placed in systematic relation plants essentially different, as now shown by comparison of their vegetative system. Moreover, they had not the advantage of a sufficiently wide knowledge of the palaeontological facts that now provide a positive check upon the conclusions which they drew. What is remarkable in the earlier groupings is that they reveal such sound classificatory instinct that, when once the priority of the Eusporangiate Ferns is conceded, the main framework of the older systems has stood the test of time, and of the wider knowledge of detail which it has brought. The amendments and reconstructions of a later day refer chiefly to the disposal of the advanced Leptosporangiates, while the more ancient families retain their identity, and to a surprising degree even the presumed relations assigned to them by the older pteridologists.

There is one conception which more than any other has affected the post-evolutionary as compared with the pre-evolutionary grouping of Ferns. It is the recognition of the polyphyletic attainment of like results. Homoplasy is written broadly across the morphology of the Leptosporangiate Ferns. The more searching the analysis the more sure will be the conclusions as to the part which homoplasy has played in any specific case. It is for this reason that the whole of the first volume of the book on *Ferns* was devoted to the recognition and investigation of the twelve criteria of comparison which were applied in the two succeeding volumes. In proportion as any suggested phyletic line satisfies the test by comparison according to a plurality, or perhaps to all of these criteria, in such measure may the conclusion that is drawn be held as trustworthy. But the facts acquired can never be exhaustive, and even the arguments may be imperfectly applied, so that the results are

doubly open to amendment. While admitting this, the soundness of the method is strongly upheld.

The grouping itself that has so far resulted is naturally incomplete. Particularly is it so with regard to the evidence drawn from the sexual generation, owing to the details being imperfectly known. It can hardly be anticipated that the gametophyte can ever challenge the sporophyte as providing material for comparison. But if the results relating to both the alternating phases, so briefly sketched here and stated at greater length in the book on *Ferns*, be taken *en bloc*, the reader cannot fail to be impressed not merely by the multiplicity of differences of detail in the several groups, but still more by the fact that certain advances in detail or character recur in so many distinct phyletic lines. In this respect the Ferns offer a field of high value to the speculative evolutionist.

The palaeontological data relating to the Ferns add more to the certainty of the phyletic conclusions than any other line of evidence. A plurality of types initiated in Mesozoic or even in Palaeozoic time, and still represented in the living Flora with essentially the same features, but with similar details of advance in each group, must be held as having been phyletic unities throughout that advance. It is here that the Filicales hold an advantage over any other Class: for, combined with the high degree of polymorphy which they present, they have a more widely illustrated and consecutive palaeontological history than any other Class of plants; moreover, they present homoplastic modifications not only in their vegetative but also in their propagative parts.

CHAPTER XXIII

THE EVOLUTIONARY RELATIONS OF THE BRITISH FERNS¹

HAVING given in Chapters XVI to XXII an organographic survey of the Filicales, and having in the last of these presented and explained a scheme of their phyletic grouping, the whole having been checked by reference to the fossil record, it seems not inapt to attempt to place the Ferns now living in the British Islands in their probable relation to the Class at large. This appears not to have been done in any published treatise. The phyletic scheme included in Chapter XXII, p. 463, will aid the attempt so far as it goes: particularly with regard to those types which are believed to be the most primitive. The types of Palaeozoic origin lie at the base of that scheme, and the first question will be, are any such still living in Britain? The Ophioglossaceae may be held as essentially palaeozoic, and the Moonwort (*Botrychium lunaria*) and the Adder's Tongue (*Ophioglossum vulgatum*) are native examples of the family. The former grows commonly among grass, and presents each year as a rule only one leaf that springs from the buried upright stock. Sometimes the leaf is sterile, showing forked venation of its pinnate lobes; but where fertile the branched ventral "spike" overtops the sterile blade, bearing its massive sporangia in regular marginal ranks, each containing a very large output of spores. In the Adder's Tongue, which is also found in grass land, both sterile and fertile parts are more compact—the former with a finely reticulate blade, the latter bearing on each margin of its simple "spike" a row of very large, laterally-fused sporangia; each of these contains spores, estimated by thousands rather than by hundreds. These peculiar plants are not such as the lay mind would readily recognise as Ferns; but detailed study, including that of the tropical genus *Helminthostachys*, suggests that the Family is really related to primitive Ferns, and in particular to the Botryopterideae which flourished in the Coal Period. Unfortunately, direct palaeontological evidence of affinity is unreliable, for early fossils referable to the Ophioglossaceae are wanting. Thus, these two species stand to-day as imperfectly modernised relics of the Palaeozoic Flora; and this is what gives them their special interest among the living Ferns of Britain.

¹ This chapter is based upon an address delivered as President of the Yorkshire Naturalists' Union, at York, 8th December, 1928.

There is, however, another Palaeozoic Fern-type which is more widely spread than *Botrychium* or *Ophioglossum*, and is far better known. The Royal Fern (*Osmunda regalis*), a denizen, though now rare, of swampy ground, is prized both for its beauty and for its toleration of domestic culture. Its thick upright stock, densely covered by masses of roots, gives rise upwards to many highly divided leaves with open venation, while the adult plant bears distally on each fertile leaf a dense truss of sporangia. These again are marginal, of relatively large size, and each produces about 500 spores. It is a noble plant, and its leaves may attain a height of six feet or more. The trunk of members of this Family appears like that of a stunted Tree Fern : it possesses in its stem and densely grouped leaf-bases a most characteristic vascular structure which finds its correlative in widely spread fossils of Permian Age. The work of Kidston and Gwynne-Vaughan on the fossil Osmundaceae has demonstrated that the type dates back to late Palaeozoic time, while sundry sporangia and sporophylls, which have much in common with those of the living genera, are frequently met with even in the Coal Measures. From such facts we may conclude that the type now represented in Britain by the Royal Fern is of Palaeozoic date.

There is one other Family represented in Britain, which has some claim to a Palaeozoic origin ; but it is rather a slender claim, suggested rather than proved : it is the Family of the Filmy Ferns, or Hymenophyllaceae, which is represented to-day by some 500 living species, of which three appear in Britain. No member of the Family is large, and some very minute ; and they are characterised by their beauty and the pellucid texture of their leaves. Among our British types the Bristle Fern of Killarney (*Trichomanes radicans*) is the largest of our three native species. It is an occasional dweller on wet shaded rocks in the West of Ireland. The more widely spread *Hymenophyllum tunbridgense* is specially interesting for its very high spore-output (256-512). The third British species is *H. Wilsoni*, common on wet rocks, particularly in Scotland. The Filmy Ferns possess one feature of definite advance on all the more ancient Ferns, in the fact that their numerous sporangia are not formed simultaneously, as they are in all really primitive Ferns ; they arise in a regular basipetal succession upon an elongated receptacle, which remains in *Trichomanes* as a persistent bristle and gives its name to the genus. The feature in the Family which attracts most attention is the thin pellucid blade, as a rule only one layer of cells in thickness. Partly on this account, partly for other reasons, the Hymenophyllaceae were long thought to represent the earliest Fern-types, being apparently most moss-like. But we now know that the filmy character is adaptive rather than fundamental, and similar filmy texture appears in certain species of *Asplenium*, *Todea* and *Danaea*, which are exposed to excessively moist conditions. The Hymenophyllaceae may thus be recognised as extreme hygrophytes ; and since no derivatives have been assigned to them they form a blind evolu-

tionary branch, the affinities of which are probably with the early Coenopterids.

It thus appears that there lives in Britain a quite respectable representation of Ferns reputed as of Palaeozoic type. Other ancient Families still exist elsewhere, and especially in the tropics, which have no living relics here. These, with the exception of the Hymenophyllaceae, all produce their relatively large sporangia simultaneously, and they may, therefore, be styled the *Simplices*. But in the Mesozoic period there was a fresh evolutionary outburst, and the Ferns took their share in it. Derivative forms arose, characterised generally by their smaller sporangia with lower individual spore-output ; also by a " *gradate* " or " *mixed* " sequence of their production. The general constitution of the plants which bore these was more delicate, their conducting tracts more highly divided, and the venation more complex, while dermal scales were substituted for hairs. These and other features marked the progression from Palaeozoic types towards those of the present day. Three intermediate evolutionary lines may be recognised, while from them we may trace finally those six large groups into which the modern Ferns can be segregated (see Scheme, Chapter XXII, p. 463). Each of these groups centres round some well-known genus, and they are accordingly named the Davallioids, Pteroids, Gymnogrammoids, Blechnoids, Dryopteroids, and the Dipteroids. Of these the first and last are not represented in the British Flora ; consequently our immediate interest lies in the remaining four.

The group of the Pteroid Ferns undoubtedly sprang from ancestors akin to the living genera *Dicksonia* and *Dennstaedtia*, which have marginal two-lipped sori showing basipetal sequence of their sporangia, borne on a receptacle which was actually marginal. The distinctive feature of the Pteroids is that the sori have lost their individuality, and are fused into series which are still borne at or near to the margin of the leaf. Though the group includes over 150 species there is only one representative in the British Flora, viz., the Common Bracken. It is often designated *Pteris aquilina*, which was the name assigned to it by Linnæus. But technically this is not correct, for it differs in essential points from that large and widely spread genus. The Bracken shares with the Dicksonioids the two-lipped sorus, the initially basipetal succession of sporangia, and the hairy covering without scales, which are all primitive features. The old generic name given it in 1760 by Gleditsch has therefore been revived, and the Bracken is now designated *Pteridium aquilinum*, Gleditsch. It is the only species of its genus, but it is a plant of cosmopolitan spread. It may be found in one or another of its various forms in Jamaica and in Ceylon ; the rhizomes of the form *esculenta* provided a staple food of the Maories of New Zealand. On our own islands it is almost everywhere. Its wide spread is probably due to its habit, with the buried rhizome well protected during its annual hibernation according to climate. Through the intermediate steps of *Paesia* and *Lonchitis* this primitive genus

is linked with the true *Pteris*, which is so remarkably successful in point of number of species, though not one of them is British. They are marked by a single-lipped sorus, which is actually superficial, and with the sporangia of divers ages intermixed, while scales appear as a dermal covering ; all these features mark advance from the state of the primitive Bracken.

It has been thought by some that the ancient stock of the Osmundaceae has no modern descendants. That may be true as regards the direct line, but there exists in the Gymnogrammoids a vast number of Ferns in which the sorus is essentially of the same type as that seen in the second genus of that Family, viz., *Todea*. The common feature is that the naked sori follow the length of the veins without any indusium at all. It is true that the Gymnogrammoids are smaller, with a lower output of spores ; but there are suggestive links in the tropical genus *Plagiogyria*, and particularly in the Mexican genus *Llavea*, which has foliage strangely *Osmunda*-like. Thus, by comparison we may reach on to our native genus *Cryptogramme*, with its well-known species the Parsley Fern (*C. crispa*), which occurs so frequently, and in quantity, in stony places on mountain sides. Or, again, to that rare annual Fern *Anogramme leptophylla*, which, as a straggler from the south, is found on the Island of Jersey ; but this is not really a British Fern, except politically. Thus again we find in the large group of the Gymnogrammoids only one truly British species. Another well-known Fern, the Maiden Hair (*Adiantum capillus-veneris*, L.), is again the sole representative of a large and widely spread genus. It nestles among limestone rocks near to the sea, a northern straggler of the so-called Atlantic Flora. Its really naked sori are borne upon the reflexed ends of its many leaf-lobes, following the veins in a truly Gymnogrammoid fashion. As in *Todea* there is no reason to believe that any of these Ferns ever had a true indusium ; their sori are, and probably always have been, superficial and unprotected. A feature that suggests their derivation from some more massive source is the instability of the annulus, combined with a relatively thick stalk, and in *Jamesonia* with a spore-count occasionally beyond 64. The whole Gymnogrammoid series presents a complex problem. It is interesting to find that our native representatives touch that problem nearly.

In certain primitive Ferns the transition of the sorus from the originally marginal position to the surface of the leaf happened early, and such a state is seen in the Gleicheniaceae, from which source a great series with consistently superficial sori appears to have sprung. The Cyatheoid Ferns were among the earlier of these derivatives, while the modern Dryopteroids and Blechnoids include most of the later developments from this source. It will be seen that we have in the British Flora a considerable representation of these superficial types ; but there is one genus which appears to be more primitive than they, viz., *Woodsia*. This genus, founded by Robert Brown, is represented in Britain by two small mountain species not readily distinguishable

from one another, viz., *W. alpina*, (Bolton) Gray (= *W. hyperborea*, Br.), and *W. ilvensis*, (L.) R. Br. Each has a short, ascending stem bearing a crown of leaves 3-6 inches high. Few would at first see in these small Ferns the northern representatives of the great Tree Ferns of the genera *Cyathea*, or *Alsophila*; but this is what they appear actually to be, as shown by the fimbriated but cup-like indusium from the centre of which rises a receptacle bearing gradate sporangia.

The Common Bladder Fern (*Cystopteris fragilis*, (L.) Bernh.), and its rarer fellow species, *C. montana*, (Lam.) Bernh., both so similar to *Woodsia* in habit, provide one of the most puzzling enigmas of relationship among our British Ferns. The question is whether their ancestry was Pteroid with marginal, or Cyatheoid with superficial sori. Here we may be satisfied in knowing that the question exists: my own opinion is the latter, viz., that, like *Woodsia*, the genus may be held as derived from some Cyatheoid source. Its spread is chiefly Northern and Alpine, but it extends also southwards through Asia, and is found in Africa and in North and South America. The Common Bladder Fern is one of our hardiest species; it is found on rocks and walls in mountainous districts, and it grows freely if planted on rockeries.¹

Turning now to the Dryopteroid Ferns, with which *Cystopteris* is probably in close relation, these are very richly represented in the British Flora. The genera *Dryopteris*, *Polystichum*, *Athyrium*, *Asplenium*, and *Ceterach* all figure among our native Ferns, and indeed form the great bulk of them. In point of their general morphology and anatomy they differ only in minor features, the distinction of the genera being chiefly according to the form of the sorus, and particularly of the indusium. The ancestral type was probably like that now seen in *Alsophila*, viz., with a naked gradate sorus, though a cup-like indusium appears in *Cyathea* and in *Woodsia*, while a laterally placed scale is characteristic of *Hemitelia*. But none of our northern types have like these attained to the stature of Tree Ferns. Probably, however, the Cyatheoids formed the starting point for all the Dryopteroid Ferns. The rare eastern genus *Peranema* gives a suggestive clue, for in it the long-stalked sorus has its indusium attached on one side only, in the form of a *cap* rather than a *cup*, though the receptacle is still radial. But in *Dryopteris* the whole sorus is lop-sided: this huge genus, with over 700 species, is a witness to its biological success. In the British Flora we have nine well authenticated species, of which the best known is the Common Shield Fern (*Dryopteris filix-mas*, Rich.). It is characterised by a kidney-shaped indusium attached by a stalk where its margin is incurved: and this suggested the old name of *Nephrodium*. But of the nine British species two are without any indusium at all, and on that account they used to be included in the genus *Polypodium*. They are the familiar Oak Fern (*Dryopteris Linnaëana*, C. Chr.), and the Beech Fern (*D. phegopteris*, (L.) C. Chr.). Their creeping habit and

¹ See *Ferns*, vol. iii., chap. xlviii.

leaf-characters are shared by other species of *Dryopteris*, and there is no doubt that they are merely species of that genus, in which, as in many others, the indusium is abortive.

In the evolution of the Ferns of this Dryopteroid affinity the sorus, and especially its indusium, have proved very plastic. We have seen that the receptacle may become lop-sided, and that the indusium may be reduced or even abortive. But these changes do not by any means mark the limit. One of the most interesting modifications is that which produces the sorus of *Polystichum*, a genus represented in Britain by the Prickly Shield Fern (*P. aculeatum*, (L.) Schott.), and the Holly Fern (*P. lonchitis*, (L.) Roth.). Here the indusium is shuttlecock-shaped, and apparently distal on the receptacle, and is seemingly very different from the basal cup of *Cyathea*. But through the intermediate state of *Dryopteris* it is easy to see how this may have come about, first by lop-sidedness of the sorus, then by a continuation of the sporangial production all round the indusial stalk, instead of only on one side of it as in *Dryopteris* itself.

A further line of modification of the sorus is based upon an accentuation of the lop-sidedness already noted. It leads through *Athyrium* to the large genus *Asplenium*, and finally with abortion of the indusium to *Ceterach*, and to "*Pseudo-Athyrium*," the so-called Alpine Polypody (*Polypodium alpestre*, Hoppe). The genus *Athyrium* itself gives the key to the change, for commonly the basal sorus of a pinnule resembles the kidney-shaped sorus of *Dryopteris*, but unequally developed on its two sides. One side is continued further along the vein than the other, while in extreme cases the latter may be absent altogether. Particularly instructive intermediate states may be obtained even from a single leaf of *Asplenium lanceum*, showing how the sorus of *Dryopteris* may pass into that typical of the genus *Asplenium*, or even of its tropical ally *Diplazium*.¹ The series thus briefly sketched is well represented in the British Flora. *Athyrium*, ranked by Hooker as a sub-genus of *Asplenium*, but now reinstated as the substantive genus *Athyrium*, Roth. 1799, appears as our Lady Fern (*A. filix-foemina*, (L.) Roth.), while the Alpine Polypody with its abortive indusium, formerly styled *Pseudo-Athyrium*, Newman, or *Polypodium alpestre*, Hoppe, now appears in its natural relation as *Athyrium alpestre*, (Hoppe) Rylands. This is a good example how the rigid observance of a mistaken systematic method may disguise true affinity, and lead to groupings that illustrate the ingenuity of the systematist rather than true relationship: for the "Alpine Polypody" ("*Polypodium*" *alpestre*) appears in the *Synopsis Filicum* over 80 pages away from its natural relative, the Lady Fern.

The genus *Asplenium*, as taken in its more strict sense, is represented by eight species in Britain, and it is fitly typified by the Common Spleenwort (*A. trichomanes*), and the Black Spleenwort, *A. adiantum-nigrum*. Abroad

¹ See *Ferns*, vol. iii., chap. xlii.

it includes over 400 species. The large and closely allied genus *Diplazium*, with over 200 species, mostly tropical, has no British type. In the calcicolous Scaly Spleenwort (*Ceterach officinarum*, D.C.) we have a single representative of a small allied genus, which differs from *Asplenium* in the venation, while the indusium shows varying degrees of abortion leading to its complete absence; these characters, together with the scaly covering of the leaves, have confirmed its separation as a substantive genus. It is thus seen that there is a rather meagre representation in Britain of the Asplenoid alliance, which is so rich elsewhere; but it serves to illustrate the natural progressions and evolutionary relations of that great body of Ferns, which are held as derivatives from a Dryopteroid, and ultimately from a Cyatheoid source.

Of the probable Cyatheoid derivatives included in the British Flora there still remain two very distinctive types, each represented by a single well-marked and well-known species, viz., the Hard Fern (*Blechnum spicant*, (L.) Wither.) and the Hart's Tongue Fern (*Phyllitis scolopendrium*, (L.) Newm.). It will be shown that the latter type is probably derived from the former. This view differs from that generally adopted: most writers have related the Hart's Tongue with the Spleenworts, a conclusion based on superficial rather than upon close comparison. The Hard Fern, though common with us in Britain and widely spread elsewhere, is the only species of *Blechnum* native in north temperate lands. Of the Blechnoid Ferns as a whole many are tropical, and a great preponderance of their species grow in the Southern Hemisphere, particularly in Polynesia. Our species is thus a very isolated type, and far removed geographically from the bulk of the Family to which it belongs. The common feature of the Blechnoids is that two linear fusion-sori take a parallel course, one on either side of the midrib, and well within the margin; while a vascular commissure, running below the common receptacle of each, supplies them in a manner not unlike that seen in the fusion-sori of the Bracken. But the Pteroids and Blechnoids are essentially different in origin, the former being types with marginal, and the latter with superficial sori. The probable origin of the Blechnoids was from types such as *Alsophila* or *Matteuccia*, with closely ranged, naked sori, forming linear series on the leaf-surface; these were linked up laterally to form fusion-sori, and covered over by the original leaf-margin, which here serves as a protective indusium (Figs. 317-319). That the type was successful is shown by the wide spread of the genus *Blechnum*, with its 140 species. They are mostly xerophytic Ferns, with tough leathery leaves, as shown in our own type, which well deserves its name of the Hard Fern.

If there were no intermediate links between *Blechnum* and *Phyllitis* our Hart's Tongue would indeed appear to be a puzzle, with its broad leaves and paired fusion-sori facing one another, each with a vascular strand below its receptacle. But the key to the puzzle is found in certain varieties of *Blechnum punctulatum* found in South Africa, supported as this comparison is by

certain related Ferns from the allied genus *Camptosorus* from North America and China. In all of these the fusion-sori do not run in straight longitudinal lines, but are thrown into sinuous curves on the widening leaf; and these are liable to interruption at the points of sharpest curvature, with the result that the isolated parts face one another just as they do in *Phyllitis* (Fig. 323). The South African variety of *Blechnum* was actually described by Kunze in 1844 as *Scolopendrium krebsii*—in fact as a Hart's Tongue. If this be a true explanation of the origin of the characteristic soral structure seen in the Hart's Tongues the genus will have had no near relation to the Asplenoid Ferns, a conclusion which exact comparison will support; for while the paired "sori" of the Hart's Tongue lie face to face, those of *Diplazium*, the Asplenoid genus with which it has been compared, lie back to back, as they naturally would if they represent the elongated sides of a single Dryopteroid sorus. Any similarity which they possess to those of the Hart's Tongue will then be homoplastic rather than phyletic.

The penultimate type of British Ferns that calls for our attention is one of the best known of all, the Common Polypody (*Polypodium vulgare*, L.): it is found on walls and banks, and it even grows epiphytically on tree-trunks in moist districts. It is a Linnæan species that has kept its name, partly because it is so well marked a plant; but the fact that it is the only true species of *Polypodium* in Europe will also have contributed to this result. Field botanists may at once object that any British Flora includes several species of *Polypodium*: Hooker includes four under that genus. But since Hooker's day it has become clear that the old comprehensive use of the name *Polypodium* to cover all Ferns with superficial, globose, and naked sori results in grouping together Ferns of quite distinct affinity. The definition implies merely a state or condition that may have been arrived at along a plurality of lines of descent. In particular, some may have had naked sori throughout their evolutionary story; others may have sori that have become naked through abortion of the indusium. This is undoubtedly the history of the Oak and Beech Ferns, and of the Alpine Polypody, which find their natural places either with *Dryopteris* or with *Athyrium*. It is quite different with our remaining British species, the Common Polypody. There is no suggestion here of an abortive indusium: it has probably had a naked sorus always, and may accordingly be retained as a true *Polypodium*, of which genus it was in point of fact the type-species. It has hitherto been placed in the sub-genus *Eu-Polypodium*, which includes various smaller, southern and tropical groups; our object will then be to decide to what affinity our isolated and sole European species really belongs.

It happens that this question, so long neglected, has recently been taken up by Dr. Carl Christensen, the distinguished author of the *Index Filicum*.¹ The typical *P. vulgare* has a creeping rhizome bearing broad scales: the

¹ *Dansk. Botanisk Arkiv.*, Bd. 5, Nr. 22, 1928; written in English.

leaves arise alternately from it, and are simply pinnate with open venation, while each naked circular sorus is borne on the anadromic branch of a forked vein. The chief variant of this usually stable type is that styled var. *Cambricum*, where the segments may be themselves once or even twice pinnatifid, chiefly in the middle region. By comparison of allied species, both from America and from Asia, Christensen has found successive steps of linking of the veins into loops characteristic of the tropical sub-genus *Goniophlebium*, and he draws the conclusion that *P. vulgare* is a free-veined *Goniophlebium*, and not a member of the sub-genus *Eu-Polypodium*, as commonly accepted. Geographically, this suggestion appears probable, for *Goniophlebium* includes numerous species in tropical America and Asia, while African and Polynesian species are few. It extends into sub-tropical and even temperate regions of Western North America and Eastern Asia, where species belonging to it meet the species *P. vulgare*, and others closely allied to it. The northern stragglers of *Goniophlebium* prove intermediate in character between the tropical species and *P. vulgare*. Accordingly we may recognise this isolated European species, our Common Polypody, as an extreme outlier of the tropical group.

Our last British Fern is the most peculiar of them all. It is the Pill-Wort, the only native representative of the aquatic Hydropterids. They include two Sub-Orders, the Salviniaceae and the Marsiliaceae; and the Pill-Wort belongs to the latter.¹ It presents a very un-Fern-like appearance, and as it grows on boggy ground, or may be submerged or even afloat, it may readily be mistaken for some Sedge or Grass, since its green leaves, borne on a creeping rhizome, are subulate; but their tips, crozier-like while young, readily betray their real nature. The most marked feature is the spherical sporocarp, which in size and colour closely resembles a compound rhubarb pill; hence the name of Pill-Wort (*Pilularia globulifera*, L.). This is again an isolated species, though it spreads throughout Europe; of the five other species only one is European, viz., *P. minuta*, found in the south of France. The probable affinity of the Pill-Wort is ultimately with the Schizaeaceae, a Family of Ferns which dates back certainly to early Mesozoic time, and was then represented in the area we now call Britain. But at the present day no representatives of the Family exist in Britain, except this rather remote derivative.

Those who have followed this examination of the Fern-Flora of Great Britain as it exists to-day will have anticipated the general conclusion to which it naturally leads: viz., that it is largely vestigial. There is an unusual proportion of species belonging to the more ancient Families; for instance, Moonwort, Adder's Tongue, and the Royal, Killarney, and Parsley Ferns. Most of the eight main groups of living Ferns are represented, but not all of them; for instance, we have no native Marattiaceae, Gleicheniaceae, or Schizaeaceae as such, though most of our native species may be held as

¹ *Ferns*, ii., chap. xxiii.

ultimate derivatives from the two last of these Families, all of which at the present day occupy stations nearer to the Equator. Further, the derivative Families of the Davallioid and Dipteroid Ferns are entirely absent, unless it be ultimately shown that *Polypodium vulgare* may be referred in origin to the latter through *Goniophlebium*. Thus, the representation of the Families of Ferns in Britain is patchy rather than complete.

Nevertheless, it is an unusually comprehensive presentment of the Filicales as a whole. The Fern-Flora of the world amounts to a total of about 6000 species, grouped in about 150 genera, and twelve Families. In Britain we have only about forty species ; but these are representative of half of those Families, and about one-eighth of the genera, while the total of our species amounts to only about one-fiftieth of the known species of the world. We may reflect how much the interest of our Ferns is enhanced by being thus distributed over so many Families, and many of these the most antique. It is probably a consequence of the position of Britain on the extreme fringe of a great continental area. If our Islands had been isolated in the ocean like the Galapagos, and had perhaps been from time to time wholly devastated by showers of volcanic ash like the Island of Krakatoa, it is highly improbable that any such inheritance of antique living forms could have been ours ; while such a Fern-Flora as might have succeeded those destroyed would probably have ranged within narrow limits ; it might, nevertheless, have had special value in relation to the origin of Species, such as the Galapagos Islands afforded to Darwin. But instead of such speculations we may dwell with satisfaction upon our native Fern-Flora as it is.

There is, however, another aspect of our Fern-Flora that is specially interesting in its bearings on past history. It arises from the fact that so many of our species occur as isolated types of Families much more extensively represented in other regions. Many even of the largest genera are with us monotypic. For instance, the Moon-Wort is our only *Botrychium* ; the Adder's Tongue is the only truly British *Ophioglossum* ; the Royal Fern is our only *Osmunda* ; the Killarney Fern is our only *Trichomanes*, and the Bracken our only Pteroid ; the Parsley Fern is our only truly British Gymnogrammoid, and the Maiden Hair our only *Adiantum* ; *Woodsia* is represented by two species, but they are closely allied and very local. The Hard Fern is our only *Blechnum*, the Common Polypody our only true *Polypodium*, and the Pill-Wort our only species of *Pilularia*. Thus, out of the eighteen genera of Ferns represented in Britain the majority are with us monotypic. So prominent a fact calls for some explanation, and two alternatives arise. We may ask ourselves whether our isolated species are, geographically speaking, feelers that have edged their way northwards, or laggards left behind when the rest of the allied species had retreated southwards, or had died out. In each case the alternative would need to be considered in the light of the facts of present-day distribution, illuminated further by palaeontological data.

Speaking generally rather than for any one instance it would seem probable that the latter alternative is correct, at least for the majority of the Ferns in question ; viz., that they represent vestiges of a richer British Flora of the past, and that the species themselves have, by their more ready adaptation or by more hardy constitution, been able to subsist in surroundings from which their congeners have retired beaten.

PART II

CHAPTER XXIV¹

ALTERNATION AND THE LAND HABIT

THE expression "Alternation of Generations" was originally applied by Steenstrup to the succession of phases seen in the life-history of Medusae, Trematodes, and other animals. He defined it as "the remarkable natural phenomenon of an animal producing an offspring which at no time resembles its parent, but which itself brings forth a progeny which returns in its form and nature to the parent animal."² Steenstrup's essay makes no reference to plants till the last paragraph, where he clearly shows that in them his comparison refers to a succession of parts distinguished after some pytonic theory, and not to the succession of generations demonstrated some years later by Hofmeister for Mosses, Ferns, and Conifers. It was natural that the later author, seeing in those plants a succession of phases superficially like those described by Steenstrup in certain animals, should have used the same general terms in describing them. But later the inexactitude of this comparison became clear. The "alternating generations" in plants differ more essentially from one another than those phases in certain animals to which the terms were originally applied.

Hofmeister's *Vergleichende Untersuchungen* were published at Leipzig in 1851. That event was duly recorded and appraised in terms of the Theory of Evolution by Sachs in his *History of Botany*.³ From that date till 1894, when Strasburger published his generalisation on "the Periodic Reduction of Chromosomes," the nature of alternation was treated rather as a question of a succession of formal events in the life-history than of inner character, or of the biological conditions under which they arose. At first the conception of alternation appeared to many as a standardised life-pattern, to which organisms of the most diverse nature possessing sexuality ought all to conform. Naturally morphology suffered by so rigid a preconception. But the whole framework of the pattern itself seemed to be shattered by the discovery

¹ This chapter is based upon the Huxley Memorial Lecture given at the Imperial College of Science and Technology, 1929, under the title "The Origin of a Land Flora, 1908-1929."

² Translation of Steenstrup's *Alternation of Generations*. Ray Soc., 1845, p. 2.

³ See the Oxford Press translation of 1890, pp. 201, 439.

of apogamy and of apospory. In 1874 apogamy was observed in Ferns by Farlow,¹ and its biological significance was discussed by De Bary.² It was thus demonstrated that a transition from the gametophyte of a Fern to a sporophyte of apparently normal type by direct vegetative growth, and without the sexual act, was not only a possible but even a recurrent event. The alternative transition from the sporophyte to the gametophyte, without the intervention of spores, to which the name of apospory is now applied, was experimentally produced by Pringsheim in certain Mosses in 1876³ and discussed in detail later.⁴ In 1884 spontaneous instances of apospory were discovered in Ferns, by Druery; and the details were at once worked out by means of cultures, so as to demonstrate that the prothalli borne on the leaves of certain wild varieties bear apparently normal sexual organs.⁵ Such facts materially altered the outlook on alternation; and it was soon found that the observed instances were not isolated, but that similar direct transitions were not infrequent in Ferns. They could even be produced or at least encouraged by suitable cultivation in them, and occasionally also in Mosses and Liverworts.

Such demonstrations directed an intensified interest upon the question of the real relations which the two "generations" bear to one another, and finally of their evolutionary origin. These questions had already been the subject of discussion, and two theories had been advanced to account for the phenomena observed. In 1874 Celakovsky distinguished three different forms of alternation.⁶ These he designated respectively: (i) the antithetic alternation; (ii) the homologous; and (iii) the alternation of shoots, or strophogenesis. The last of these calls for no detailed treatment here. It refers to such phenomena in plants as were discussed by Steenstrup in animals; as we have seen he definitely compared them in his last paragraph with the alternation of shoots seen in the sporophyte, and particularly in that of Flowering Plants. The interest therefore centred on the other two types. By antithetic alternation he connoted the result of interpolation of a new phase between successive gametophytes in the course of descent, and to this origin he attributed that succession of alternating phases (*Biontonwechsel*) which makes up the cycle of Archegoniate Plants. Under the head of homologous alternation he ranged the succession of phases seen in the Algae and Fungi. The terminology used was not explicit even in 1874: for Ray Lankester had already pointed out in 1870 that the word "homologous" has a double significance.⁷ If it be used to connote examples of what he styled

¹ *Bot. Zeit.*, 1874, p. 180.

² *Bot. Zeit.*, 1878, p. 449, etc.

³ *Monatsbr. K. Akad. Wiss.*, Berlin, Juli 1876.

⁴ *Pringsh. Jahrb.*, xi., 1877, p. 365.

⁵ Druery, and Bower, *Linn. Journ.*, 1884, pp. 354, 360; Bower, *Trans. Linn. Soc.*, 1887, p. 301.

⁶ *Bedeutung des Generationswechsels der Pflanzen*, Prag., 1874.

⁷ *Ann. and Mag. of Nat. Hist.*, vol. vi., p. 34.

"homoplasmy" the whole field would be open for including what has been called antithetic alternation, in which the two generations are presumed to be homoplastic. If in the sense of "homogeny" then it would be necessary to prove the relation of the "bionts" throughout descent to the sexual cycle. On the other hand the term "antithetic," while it accentuates the difference between the two "bionts," is not explicit, in that it does not specify the method believed by its adherents to have been involved in their origin. It would be well to drop these old terms and to substitute the words "*interpolation theory*" in place of "antithetic," and "*transformation theory*" in place of "homologous." These words are explicit in conveying the alternative methods of origin.

Close on the heels of Celakovsky followed Strasburger (1874),¹ and Pringsheim (1876, 1877).² The latter approached the problem partly through experiment, partly from his wide knowledge of the lower forms of vegetation. In the first place he had already demonstrated that, on suitable culture, pieces of the seta of a moss-sporogonium may produce protonema and moss-plants by purely vegetative growth: in point of fact by aposporous growth from internal tissues; and this appeared to him to favour an homologous transformation.³ Strasburger, on the other hand, concluded from comparison that for all plants, from the Mosses upwards, it appears probable that we have to do merely with a differentiation of a single generation: that is, with a strophogenesis. Upon the conflicting issues thus stated a lively controversy developed, chiefly on the basis of form rather than of inner difference or origin.⁴ It soon lost its intensity in face of the obvious deficiency of such facts as alone could lead to some final conclusion.

But in the course of the discussion a biological rather than a purely morphological turn had been given by reference to the amphibial life shown by the Archegoniatae, which formed the primitive Flora of the Land. This was introduced in 1890.⁵ It was presumed that they sprang from green aquatic forms, inhabiting shallow fresh water or the higher levels between tide-marks; that sexual reproduction was effected through the medium of external liquid water, and if other conditions were favourable it could be carried out at any time by such Algae, provided water be present and the sexual organs mature. But certain forms, perhaps thereby escaping competition, established themselves on land where access to liquid water was only an occasional occurrence. In these the sexual process could only be effected

¹ *Jenaische Zeitschrift*, 1874, p. 69.

² *Pringsh. Jahrb.*, xi., p. 365.

³ In 1901 Lang made similar cultural experiments on parts of unopened sporogonia of *Anthoceros*; with the result that thalloid growths with rhizoids sprang from internal cells lying between the sporogenous layer and the epidermis; he concluded that the growths were aposporous. *Ann. of Bot.*, vol. xv., p. 503.

⁴ Scott, Address to Sec. K Brit. Association, Liverpool, 1896. Bower, Address to Sec. K Brit. Association, Bristol, 1898.

⁵ Bower, *Ann. of Bot.*, vol. iv., p. 347.

at time of rains or copious dews. Thus, less dependence could be placed upon sexuality for propagation, and an alternative method of increase of individuals had to be substituted. This was done by the production from the zygote, or fertilised egg, of a new phase, now styled the sporophyte. Once fertilised the egg might divide, giving rise to a number of portions, or carpospores, each of which would then serve as a starting-point for a new individual: and dry conditions would favour the dispersal of the powdery spores. The more numerous the spores the greater the probability of survival and of spread. But increase in the number of spores entails increased nourishment; accordingly in the higher forms the sporophyte itself assumed the function of nutrition, developing high morphological differentiation of its parts. This would lead finally to the independence of the sporophyte from the gametophyte that bore it, as a free-living plant with root, stem, leaf, and sporangium as its distinct members. Thus the morphological fixity of the alternation explains itself as an interpolation that is historically probable, for it would be biologically efficient. Given a conservatism in the mode of fertilisation, which was assumed to have been inherited from an algal ancestry, the rise and progress of the sporophyte in the Archegoniatae were regarded as the natural outcome of a migration from water to land, and it was held to have been carried out by organisms all of which had a full green colour.

Into the dying embers of the formal controversy on alternation, thus vivified by a biological commentary, Strasburger dropped as a bombshell his generalisation on the Periodic Reduction of Chromosomes.¹ The explosives had been gradually acquired by the exact cytological analysis introduced by Strasburger himself. In 1893 Overton had already suggested a cytological distinction between the alternating generations;² but it remained for Strasburger to formulate the generalisation that a chromosome-cycle is general for the life-history of plants showing sexuality; and that its critical points lie in syngamy, resulting in a doubling of the chromosome-number, and meiosis or reduction, the result of which is to halve that number. The immediate effect of the theory was to stimulate observation, and the earliest test-cases were Algal: viz., *Fucus*³ and *Dictyota*,⁴ in both of which a normal nuclear cycle was demonstrated. Since then the confirmation has been widespread, so that it may now be stated generally that the sporophyte is normally diploid ($2x$), and the gametophyte haploid (x).

At first sight it appeared as though this chromosome-distinction had at last supplied some inner but tangible distinction between the two generations, which would serve as a safer criterion than mere external form, or tissue

¹ Brit. Association, Oxford, 1894.

² *Ann. of Bot.*, vii., p. 141.

³ Strasburger, *Pringsh. Jahrb.*, 1897; Farmer and Lloyd-Williams, *Phil. Trans.*, B., 1898.

⁴ Lloyd-Williams, *Ann. of Bot.*, xi., 1897; xviii., 1904, p. 141.

construction. Moreover, observations of the cytological detail soon showed in a vast number of normal life-histories that the chromosome-distinction was very strictly maintained. It was found to apply equally for certain Algae, for the Archegoniatae, and for Flowering Plants. But this only served to concentrate attention upon those abnormalities already described as apogamy and apospory. A number of examples, particularly in Ferns, have been worked out cytologically, with surprising and various results. For instance in *Marsilia Drummondii*, where an apogamous embryo is developed from the ovum though fertilisation is prevented by the failure of the archegonium to open, the cycle was found to be diploid throughout.¹ The same cytological condition was demonstrated for *Athyrium filix-foemina* var. *clarissima*, Bolton, by Farmer and Miss Digby.² On the other hand, in *Lastraea pseudo-mas* var. *cristata-apospora*, Druery, the same authors concluded that the gametophyte-character had been impressed upon the sporophyte, and a similar condition was shown by Yamanouchi in *Nephrodium molle*,³ and by Steil for *Nephrodium hirtipes*, Hk.⁴ Thus it was seen that the gametophyte may be diploid though normally it is haploid; and that the sporophyte may be haploid though normally it is diploid. In neither case did the cytological difference appear to affect the form or structure of the parts in question. Hence the conclusion drawn by Farmer and Miss Digby was, that no necessary relation exists between periodic reduction in the number of chromosomes and the alternation of generations. That conclusion appears to be fully justified from these and many later observations made upon rather advanced Ferns now living. But it may be doubted whether it has any direct bearing upon the question of the prime origin of alternation. In face of the prevalence of the cytological condition that is held to be *normal*, over these exceptions, it seems justifiable to conclude that they are relatively late and isolated departures from an originally normal state in which a periodic reduction was the rule. Notwithstanding their frequent occurrence under present conditions the regular cytological cycle may be held as the normal for the Archegoniatae, and particularly for their most primitive types.

The difference in proportion of the alternating phases in Bryophytes and Pteridophytes was a familiar fact from the first: the gametophyte preponderating in the former and the sporophyte in the latter. Botanists were hardly prepared, however, for those marked differences which were disclosed when the Algae were cytologically examined. It has been demonstrated by many recent observations on Algae how unstable are the proportions of the two alternating phases in them: even the existence of a somatic alternation, as distinguished by cytological detail, may be absent. A few outstanding examples may suffice. Among the Brown Algae the plant of *Fucus* has proved

¹ Strasburger, *Flora*, Bd. xcvi., p. 123.

² *Ann. of Bot.*, 1907, p. 161.

³ *Bot. Gaz.*, 1908, vol. 45, p. 289.

⁴ *Ann. of Bot.*, 1919, p. 109.

to be constantly diploid, and there is no somatic alternation.¹ More recently such an alternation has been demonstrated in *Laminaria*, though with great difference in the relative size of the alternating phases.² Nevertheless, a cytologically distinct and evenly balanced alternation is seen in *Dictyota*.³ Thanks to the researches of Dr. Knight on *Pylaiella* we now know that "homologous" alternation exists in that simple filamentous Brown Alga. This example serves to show how easily a cytologically distinct alternation can arise in lowly filamentous types.⁴ It is possible that analogous cases are yet to be discovered in the Chaetophorales: also in other Green Algae which are under examination on this point.⁵ Among the Red Seaweeds a cytological alternation of two somatic phases has been fully made out by Yamanouchi for *Polysiphonia*.⁶ But Svedelius showed in 1915 that the plant of *Scinaia* is haploid throughout, and that there is no diploid phase, reduction taking place in the first division of the zygote.⁷ Divergent observations of this nature, now widely verified in other types, led Svedelius to distinguish between *haplobiontic* and *diplobiontic* life-histories in Algae, and to the recognition of the fact that in them it is necessary to discriminate between alternation of generations distinguished according to form or succession of phases, and alternation of the nuclear state. Both may coincide, as they normally do in the Archegoniatae; but this is not universally obligatory. On the basis of such facts as have been quoted, Oltmanns has summed up the question for Algae at large as follows: ⁸ "That the process of reduction of chromosomes in the Algae has nothing whatever to do with alternation of generations. That process is inevitably determined by the sexual act; but in the Algae it is carried out at a point in the cycle of development that is not always the same." Biologically this conclusion may be related to the fact that Algae, having been evolved under the equable conditions of aquatic life, have been given relatively free play in the adjustment of their somatic phases upon the nuclear cycle. It becomes, indeed, an open question whether the Algae, having that latitude of adjustment, can be any trustworthy guide for comparison of somatic development in the amphibious vegetation of the land. On this point Oltmanns has remarked that "when we affirm that an alternation of a gametophyte and a sporophyte is seen in the more highly developed Algae, that is not the equivalent of saying that all the forms cited betray an

¹ Strasburger, *Pringsh. Jahrb.*, 1897; Farmer, *Phil. Trans.*, B., 1898.

² Kylin, *Ber. Deutsch. Bot. Ges.*, xxxv., 1917, p. 298.

³ Lloyd-Williams, *Ann. of Bot.*, vol. xi., p. 545; vol. xviii., pp. 141, 183; vol. xix., p. 531.

⁴ *Trans. Roy. Soc. Edin.*, liii., 1923, p. 343; also lvi., 1929, p. 307.

⁵ Fritsch, Address to Section K Brit. Association, 1927; also Schüssnig, abstracts Int. Bot. Congress, Cambridge, 1930, p. 189.

⁶ *Bot. Gaz.*, 1906, p. 401.

⁷ *Nova Acta Reg. Soc. Upsala*, 1915, vol. 4, No. 4.

⁸ *Morph. und Biol. d. Algen.*, Bd. iii., 1923, p. 138.

affinity to the Archegoniatae. Just as sexuality may be held to have arisen repeatedly and independently in various groups of the lower organisms, so may the various higher families have carried out independently the establishment of two generations."¹ In the problem of the origin of a Land Flora his argument leads to this: that *the alternation of generations seen in the Archegoniatae will have to be discussed on its own merits*. The fact that there is a cytologically diploid phase in *Dictyota* or in *Polysiphonia*, or in any other Alga, does not imply homogeny with that of any one of the Archegoniatae. It merely indicates that *homoplastic post-sexual phases have been developed in widely different plants*. Continuing this line of thought Von Goebel remarks that "it is not possible to bring any one family of living Thallophytes into genetic relation with the Archegoniatae";² and, further,³ that "the advance made in recent years in the study of alternation consists in this: that it is recognised that the doctrine of alternation founded originally for the higher plants (from the Bryophyta upwards), cannot be extended to all plants."

With the ground thus freed from the trammels of an assumption that alternation in distinct classes of plants was essentially of one type, we may turn to an enquiry into the foundations upon which the origin of the alternation seen in Archegoniate plants may be based. We may agree with Fritsch that it does not seem natural to seek the origin of green terrestrial plants in relation to any of the Brown or Red Algae, but rather among those possessing the same plastid pigments and the same metabolism as theirs. We may even concentrate on the Isokontae, though the most elaborate of them are but little advanced from the filamentous state, and stop short of a massive plant-body. Fritsch asks pertinently, what has become of any more elaborated members of the Class? He suggests that at about the evolutionary level of the differentiated filament a transition to terrestrial life took place, and that there are no higher Isokont Algae because they have become land-plants.⁴

Be this as it may, his suggestion turns special attention once more to the post-sexual phase. Such Green Algae as *Ulothrix*, *Coleochaete*, and *Chara* stand cytologically on the plane of the haplobiontic seaweeds, meiosis being involved in the first division of the zygote. None of these seems to have hit on the innovation of postponing meiosis by interpolation of a diploid phase. On this point the plants named have preserved a stolid conservatism that has resulted in evolutionary inertia. Here lies the biological gap between green aquatic and green amphibian life. But if any race of amphibial plants were to have initiated such a diploid phase as sub-aerial plants possess, what a future would have opened before it! Nothing less than the capture of the land, provided that the diploid phase were fitted to endure sub-aerial life, and were protected against the risks of youth, as the Archegoniate embryo

¹ *l.c.*, p. 143.

² *Organographie*, Teil i., 1928, p. 526.

³ *l.c.*, p. 530.

⁴ Address to Section K Brit. Assn., 1927.

is. It will be well to enquire whether any biological circumstances or any observed structural facts would make so important an advance seem probable.

Upon the facts relating to haplobiontic organisms, such as *Scinaia*, Svedelius has founded a new biological theory of the origin of a sporophyte, and it is applicable to all plants in which syngamy is followed sooner or later by the production of carpospores. Moreover, it applies independently of the external conditions of life.¹ He holds that the main significance of meiosis lies in making new combinations in the daughter-nuclei possible. Reduction is to be regarded as the final act and goal of fertilisation. With each number of chromosomes a certain number of combinations will be possible: of these, two at most can be realised at each tetrad-division. Consequently when meiosis follows at once on fertilisation there is only one spore-mother-cell, and only one tetrad-division, so that no more than two chromosome-combinations can possibly result. But when a more highly developed diploid sporophyte is formed, with numerous spore-mother-cells, numerous combinations will be realised. Thus by postponing the event of meiosis, by somatic interpolation and increased facilities for a large spore-output, the plant multiplies its chances of forming new combinations of heritable characters. This theory of Svedelius in no way supersedes the biological advantage following on a large spore-output in amphibious plants (Bower, 1890): the two factors would indeed co-operate in promoting the success of an enlarging sporophyte. In fact, the theory appears to strengthen the probability of interpolation by giving an intelligible reason for its initiation; moreover, it may be applied either for submerged Algae or for plants of the land, though not equally as regards the advantages gained: the greater advantage would rest with the latter.

The detailed change by which delay in the act of meiosis could be carried out is the simplest possible. It would consist normally in a continuance in the growing zygote of vegetative division similar to that which produced the gametes themselves, but with a diploid in place of a haploid structure: meiosis and spore-formation, though delayed, would still be the final result. In point of fact, intermediate steps between Green Algae and the amphibial Archegoniates have not been demonstrated in the flora of the present time. It might therefore appear that the suggestion that such interpolation, with delayed meiosis, ever took place was without foundation in fact; were it not that the change from spore-mother-cells to a sterile state is of frequent occurrence in land-living plants, from the Bryophytes upwards. Many instances from Archegoniate and from Seed-Bearing Plants are quoted in Chapter VII of *The Origin of a Land Flora*, under the heading of "Sterilisation." This conversion of potentially fertile cells into vegetative cells was recognised by Naegeli, and embodied by him in his fundamental

¹ Svedelius, *Ber. d. D. Bot. Ges.*, 1921, Bd. xxix., Heft 5; also *Bot. Gaz.*, 1927, vol. lxxxiii., p. 362.

law of organic development, as follows : " The phenomenon of reproduction of one stage becomes at a higher stage that of vegetation. The cells which in the simpler plant are set free as germs, and constitute the initials of new individuals, become in the next higher plant part of the individual organism, and lengthen the ontogeny to a corresponding extent." ¹ Thus it is seen that the interpolation of a neutral diploid phase into the life-cycle of a haplobiontic organism would be a phenomenon cognate with Naegeli's fundamental law of organic development. Further, the conditions of amphibial life of the early Archegoniates, as explained above (pp. 485-6), would be such as to encourage the development of the sporophyte. The prevalence of the results of interpolation in Archegoniate plants is itself evidence that the developing sporophyte had survival value. This has, in fact, sufficed to standardise it in the amphibial life-cycle of the Archegoniatae, in contrast to the relative instability presented by the life-cycles of Algae.

The considerations advanced in the preceding paragraphs appear to justify the suggestion that the remote ancestors of the Archegoniatae were haplobiontic, as are certain Green Isokonts, many of which are littoral, or even sub-aerial. At first meiosis may have followed directly on syngamy, as in the Haplobionts generally. By deferring the act of meiosis, and interpolating by progressive growth and sterilisation a post-sexual diploid phase, which is wanting in those living Isokonts, the advancing Archegoniate type would at one stroke achieve three biological ends of supreme importance to any land-living organism : (i) a multiplication of possible combinations of hereditary characters, giving the raw material for variation ; (ii) an opportunity for securing a wide spread on dry land by the dissemination of numerous air-borne spores : (iii) relief from dependence on repeated syngamy for numerical increase on land, where the necessary medium of external liquid water is not always available. This last end was probably the most important of all for land-living plants. The superiority thus gained by the early plant-amphibians, combined with their embryogeny protected by the venter of the archegonium, will have favoured a rapid advance of the sporophyte. The haplobiontic ancestors would be left hopelessly behind, as are the present Green Algae. The result would then be what we actually see : viz., a wide gap in point of form and constitution between these and their successful progeny. The theoretical position thus adopted for the Archegoniate Plants of the Land is substantially the same as that developed in 1908, in *The Origin of a Land Flora*. *It is still held that the Archegoniate sporophyte, or diplophase, is a stage interpolated in the course of evolution between the successive events of syngamy and meiosis ; and that the neutral somatic development is not strictly homogenetic with the sexual, though both are phases of the same ontogenetic cycle.*²

¹ *Abstammungslehre*, p. 352.

² This position was explicitly stated in *A Course of Practical Instruction in Botany*. Macmillan, 1891, p. 341, footnote.

But the retention of this position for the Archegoniatae does not prevent the recognition of other forms of alternation in other Classes of Plants. For instance, it seems fully made out that in certain Algae alternation by transformation has taken place. This need not raise any difficulty, for there is no justification for assuming that all organisms should present a uniform type of life-story, or one evolved along one uniform channel. It is biologically improbable that they should when the medium in which they have evolved is as different as that between submerged and sub-aerial life. The problem

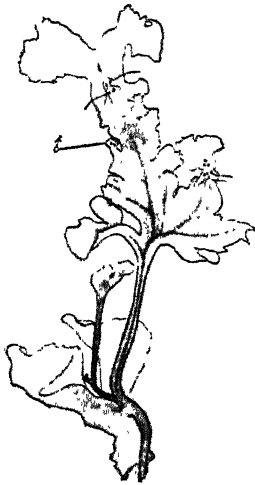


FIG. 388.

Nephrodium pseudo-mas v. *cristata* (Cropper). Drawing by Dr. Lang, showing apogamous transition from prothallus to sporophyte, and subsequent aposporous transition to prothallus at the apex and margins of the leaf.

before the nascent plant has been to adjust somatic development with its nutritional function to the nuclear cycle with its leading events of syngamy and meiosis. But somatic development and the nuclear cycle are essentially different things. The somatic phases are of the nature of plastic biological accommodations: the nuclear cycle involves a sequence of events inexorable in their normal succession, however variable in their incidence. There is no ground for assuming that the two should be interlocked in any rigid scheme. It is true that the events of both orders may in certain cases coincide in their succession, as they do normally in the Archegoniatae; and it was in these that alternation was first demonstrated. But in the Thallophytes there may be, and there are misfits. The fact is that the old controversy between the adherents of "antithetic" and "homologous" alternation arose from an ill-judged attempt on both sides to interpret all life-histories, whether aquatic, amphibial, or sub-aerial, according to one

scheme. It now appears that if this attempt be abandoned both sides may claim to have been right; but neither universally so. The adherents of "antithetic alternation" will find illustrations of their view centred in the Archegoniatae, and in the Land-Flora at large: those of the "homologous alternation" must be content to find examples that justify their view among the Thallophytes.

The foregoing discussion will have tended to contrast the two alternating phases of the Archegoniatae, accentuating their distinctness: they are recognised as homoplastic rather than homogenetic, but still they are parts of one life-cycle. On the other hand many recent observations, whether based upon naturally produced specimens or on the results of cultivation and experiment, have tended to minimise any sharp distinction between them. Apogamy and apospory are of frequent occurrence, and are not uncommonly combined in

the same ontogenetic cycle : for instance in the young apogamous plants of *Nephrodium pseudo-mas* v. *cristata*, where the leaf hastens to the production of new prothalli by direct outgrowth of its margin (Fig. 388). A similar example is described by Von Goebel in *Pellaea flavens*, where a prothallus is continued upwards into a cylindrical body with hairs and stomata, and terminates again in a prothallus with antheridia.¹ As showing that such aberrant development is not restricted to advanced Leptosporangiates, Lang has recorded in young plants of *Osunda* a high degree of flexibility in the development of shoots, leaves, and prothalli on the single young individual.² A consequence of such irregularities may be an abnormal juxtaposition of gametangia and sporangia, as has been demonstrated by Lang in *Scolopendrium* and *Nephrodium*³ (Fig. 388 bis). Frequently, however, such organs are imperfect. The climax of abnormality is reached when sperms are found to replace the contents of an organ that is clearly a sporangium : as seen in varietal hybrids of *Scolopendrium vulgare*.⁴ Such instances quoted from a great volume of recorded fact serve to illustrate some of the present-day departures from the normal " Hofmeisterian " cycle in Archegoniatale life-histories. They are not infrequent, and may arise in Nature, or be experimentally induced. By putting together selected examples it might be possible to present very varied types of life-cycle.⁵



FIG. 388 bis.

Nephrodium dilatatum, Desv., var. *cristatum gracile*. Prothalloid cylindrical process, bearing archegonia near its base. It arises by the side of an imperfect sporangium (sp), and bears a similar sporangium (sp) on the other side, and on the tip are a number of sporangia associated with rameta. $\times 35$. (After Lang.)

¹ *Organographie*, Teil i., 1928, p. 535, Fig. 555.

² *Proc. Manch. Lit. and Phil.*, 1924, vol. 68, p. 63.

³ *Phil. Trans.*, B., 190, 1898.

⁴ Miss Gairdner, *Nature*, 1933, p. 622, with figures.

⁵ A full bibliography up to 1908, relating chiefly to apogamy, is given by Winkler (*Progressus Rei. Bot.*, vol. ii., p. 444). More recent records, especially for apospory, will be found in works on cytology. Reference should also be made to *Ferns*, vol. i., chap. xvi., where irregularities of the life-cycle are discussed, with citations of literature.

It may, however, be questioned whether these would represent any state which ever held a place in evolutionary history. The warning of a former generation of botanists, in reference to the monstrosities of Flowering Plants, is equally apposite to these organographic and cytological events of the present day. Von Goebel remarked in 1884¹ how important is the study of the factors which bring abnormalities into existence ; and how without this the study of teratology becomes discredited, a result that has often followed. For, as A. de St. Hilaire says,² without this condition monstrosities would favour equally all the vagaries of imagination ; and, as Henri de Cassini remarked, "one might see in them whatever one wished to see." The caution thus advised in the last century is equally necessary to-day in treating the abnormalities of the Archegoniatae in their bearing on alternation, and their comparison with the less stable life-cycles of Algae.

An old principle in morphology has been to fix upon the most constant features, and to give them precedence over those that are variable. The most stable feature in plants possessing sex is the alternate succession of correlated events known as syngamy and meiosis. These events exist in the life of unicellular organisms, which indicates that they are not necessarily dependent on somatic phases ; hence it follows that the critical events of the cytological cycle take precedence over them in morphological comparison. Further, if the events of syngamy and meiosis have been constant throughout normal descent, the two somatic phases will each have had a separate phyletic origin. They may or may not have coincided in time of first appearance, but the existence of haplobiontic Algae suggests that in certain cases they did not. Their initial form will probably have depended upon the external conditions. Such reflections give a natural setting for the discussion of alternation whether normal or abnormal, as seen in Archegoniate Plants. As the result of wide comparative study of the Archegoniatae, with all their differences of detail, Von Goebel has laid his finger upon an important starting point of their comparison. He directs particular attention to the fact that, whether in Bryophytes or Pteridophytes, those forms which stand earliest in their respective series are those in which the difference of the alternating phases is least marked. He quotes as examples the Anthocerotales among the Bryophytes, and among the Pteridophytes the Lycopodiales.³ These in conjunction with the Psilotales and some of the earliest types of Filicales form a more or less coherent central plexus of primitive types of land-vegetation. Such similarity as their haploid and diploid phases show, and particularly those of the Anthocerotales and Psilotales, suggest that the two generations started under like conditions, and that both were of somewhat similar form, and photosynthetic. But there is no direct evidence

¹ "Vergl. Entwicklungsgesch." : Schenk's *Handbuch*, iii., p. 125.

² *Leçons de Botanique*, p. 824.

³ *Organographie*, 3rd ed., p. 537.

for the priority of either, though much indirect suggestion that the gametophyte was earlier established than the sporophyte. A circumstance that will have had wide morphological consequences in differentiating them was the adoption of the nursing habit within the archegonium.¹ This innovation once established has become a fixed feature of land vegetation ; but it will have tended to obliterate detailed evidence of initial steps. Each somatic phase would then specialise along the divergent lines of nurse and offspring. All this would fall within that ambit of events which may be called the " Hofmeisterian " cycle. Its *high degree of standardisation* for primitive land plants is still so far preserved that it may be recognised as the *normal*. But there is no reason to expect that the normal cycle should always be retained to type, though it is so in the vast majority of individual Archegoniatae. *Deviations are numerous and varied; but they are not standardised as the normal cycle is.* Hence it may be concluded that such deviations—which bear all the signs of individual adjustment, and are in some degree capable of being produced at will by experiment—are *ex post facto events*. They illustrate the potentialities of plants of the present day rather than evolutionary features of the remote past, and will have played no part in producing that normal alternation which is characteristic of the Archegoniatae.

In conclusion, the attempt should be made to relate this discussion to life at large, by comparing the two Kingdoms of living things in respect of alternation. In both a cytological cycle exists wherever there is sexuality, with syngamy and meiosis as its essential events. According to the view here entertained two opportunities for development of a vegetative phase are present in each cycle : the one may produce a haploid body intervening between the events of meiosis and syngamy ; the other a diploid body appearing between syngamy and meiosis. All the highest developments in either Kingdom are products of a diploid body ; in this fact we see a full justification of the theory of Svedelius, for the highest structure is thus associated with the means of multiplication of cytological combinations of heritable characters. But this result has been attained differently in the two Kingdoms. In Animals it was achieved, so to speak, by first intention. In them the whole somatic development was from the first diploid, and a haploid body was not advanced beyond the unicellular stage. Thus there never was any alternation of actual phases or generations in Animals in the Hofmeisterian sense of the word.

In all the higher Plants both opportunities were put in actual practice, and a true alternation has been the result. There is reason to believe that in the first instance the haploid phase or gametophyte was developed ; but so long as the zygote underwent direct division as a spore-tetrad only two distinct combinations of heritable characters could result from each completed

¹ Lang, *New Phyt.*, vol. viii., 1909, p. 104.

cycle. This is the case for all haplobiontic organisms which possess a gametophyte, but no somatic sporophyte. Subsequently, however, and particularly in the Archegoniatae according to the theory advanced here, a sporophytic phase or generation was interpolated in each life-cycle between the successive gametophytes. Numerous hereditary combinations were thus secured, as they were from the first in Animals. In land-vegetation this later phase has attained such preponderance that the original gametophyte has been overshadowed by it, and virtually eliminated. Thus, notwithstanding their false start as compared with Animals, Plants have finally, by a kind of evolutionary after-thought, attained a like result with them; and the diploid plant-body, though secondary in its origin, now constitutes to all intents and purposes the Vegetation of the Land.

It thus appears that there are three forms in which somatic development may be related to the nuclear cycle characteristic of all organisms possessing sexuality. (i) That in which a haploid soma intervenes between the events of reduction and syngamy: this is characteristic of haplobiontic Algae. (ii) That in which there is present not only the haploid phase, as before, but also a diploid phase which intervenes between the events of syngamy and reduction: this is characteristic of the Archegoniatae, and the derivative Seed-Plants: it is also seen in many Thallophytes. And (iii) that in which a diploid soma intervenes between the events of syngamy and reduction, but there is no haploid soma: this is characteristic of Animals. The fact that the haploid phase may exist without the diploid, while the diploid may exist without the haploid, appears to strengthen the view that the two phases seen in the Archegoniatae differ in the history of their origin; and to support for them the theory of interpolation, of which that historical difference is the essential feature.

CHAPTER XXV

PROTHALLUS AND GAMETANGIA

IN the last Chapter the gap between the Chlorophyceae and the Archegoniatae has been fully recognised, and no attempt need be made to draw its margins theoretically nearer together than the facts will allow. Yet we may carefully examine either side of the gap, and particularly the Algal side, before proceeding to the comparison of the gametophyte in the Archegoniatae. The "plant" in the Chlorophyceae is commonly filamentous.

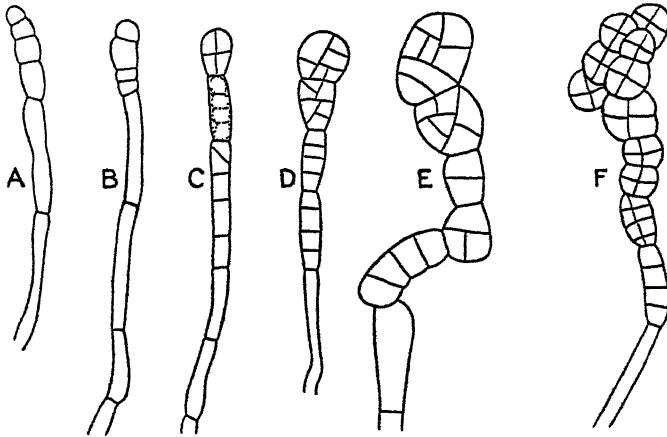


FIG. 389.
Frittschiella tuberosa. Various stages of growth of the young plants. $\times 400$. (After
M O. P. Iyengar.)

Some concrete example will show how far one of them may correspond structurally to the haploid phase of Archegoniate plants. An amphibial Alga referred to the Chaetophoraceae has lately been described from Mysore, named *Frittschiella*, which appears gregariously on moist silt in pools drying up after the monsoon.¹ The young plant consists of a simple upright filament, the lower part rhizoidal and sometimes branched (Fig. 389, A-C) : the cells of the upper part grow and divide, mainly by walls at right angles to one another, forming a group of rounded cell-clusters ; together they constitute a system which may branch irregularly (D, F). From these

¹ Iyengar, *New Phyt.*, xxxi., 1932, p. 329.

clusters upright, sparsely-branched filaments arise, the distal cells of which are elongated, with bright green contents. The whole may be attached to the soil by additional septate rhizoids (Fig. 390). The motile stages of this Alga are not yet known. Its interest lies in the terrestrial habit, and in the fact that this amphibial plant possesses the essentials of a three-dimensional, photosynthetic sub-aerial thallus originating from a simple filament.

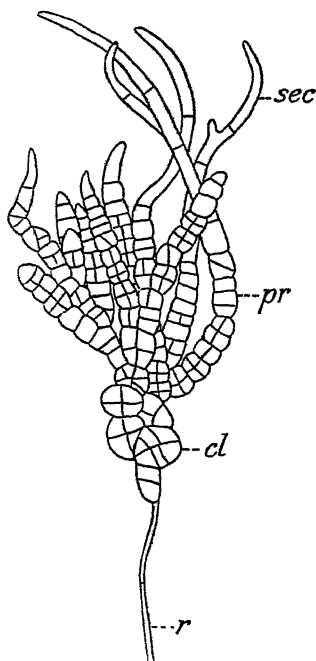


FIG. 390.

Frittschiella tuberosa. A small mature plant with a single rhizoid. *cl* = cluster; *pr* = primary; *sec* = secondary branch. $\times 350$. (After Iyengar.)

The living Chaetophorales, to which *Frittschiella* belongs, are distinguished by a capacity for existence under varied conditions that is in advance of any other group of the Isokonts. Within this Class almost every conceivable type of simple plant-body has been realised, and is still existent. But the development stops short of a massive parenchymatous construction.¹ The crude materials are present in Fig. 389 for the organisation of a higher vegetative development on land, such as the Archegoniatae possess. What is lacking in the gametophyte of these green terrestrial Algae is further massive development, and localisation of growth. It is upon these factors that the evolution of the haploid phase in the Archegoniatae has been mainly founded.

It must suffice very briefly to mention the Charales, as a phylum of Green Algae of very ancient origin, which have taken an independent line of elaboration of their own, though they present interesting analogies with other aquatic or amphibial plants. Their usual habitat of shallow fresh water is liable to seasonal drying, and certain structural features accord with this. The plant is haploid, and as the reduction follows in the first division after syngamy there is no diploid soma. In this the Charales are on the same level as other haplobiontic Algae, and particularly the Isokonts. There are points of interest in the vegetative development of the gametophyte, which, notwithstanding some degree of structural complexity, is throughout based upon the septate filament, with frequent characteristic branching. Cortication is present in the main stem of *Chara*, which is not unlike that seen in certain Red and Brown Algae. But the chief interest centres in the protection of the gametangia. Morphologically the "nucule" may be held as a distal oogonium containing a single matured ovum, and protected by closely appressed branchlets correlative with those which form the cortex of the stem in *Chara*. The "globule" or an-

¹ Fritsch, Address Sec. K, Leeds, 1927.

theridial branch cannot be so simply analysed. Whatever the morphological nature of the coverings of the gametangia, the biological interest lies in the fact that they are protected in this amphibious organism. The gametes themselves, and particularly the egg after fertilisation, present a problem common to all sub-aerial life. The protection of the egg in the Charales is achieved in a different way from that in the Archegoniatae; but the requirement is the same for both, though the response has been clearly homoplastic.

The foregoing paragraphs will have suggested, from the Algal side, a general point of view of the biological state in such plants as live "between wind and water." They show how certain Green Algae have reacted to amphibial life, but only within a narrow margin of adaptation. In the Archegoniatae such adaptation is very much more advanced, and it has dominated their morphological character, with the result that they are successful as land-living plants. Difference in adaptability rather than in the character of the adaptation may account in some measure for the divergence between any Green Alga and any Archegoniate. This difference accounts in the Green Algae for the lack of that co-operative adaptation of both phases to life on land which appears in the Archegoniatae. In particular, the protection of the ovum in the latter by a somatic growth derived from the gametophyte gives the characteristic feature of the archegonium. But in the amphibial Green Algae this is only distantly adumbrated by the "nucule" of the Characeae, or still less perfectly by the protective filaments surrounding the zygote of *Coleochaete*.

In many of the living Archegoniatae the gametophyte starts as a simple filament: in others it takes at once a more advanced form. Where present the simple filament usually expands upwards, as in *Riccia*, into a massive parenchymatous structure (Fig. 391). Differences in behaviour of the sporeling on germination are illustrated by Campbell's drawings in *Mosses*

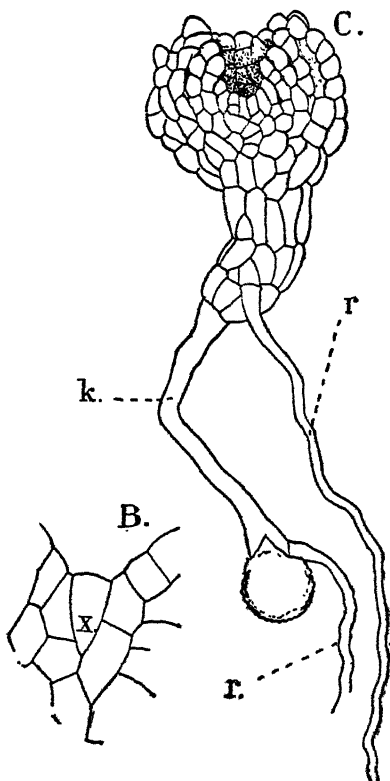


FIG. 391.

Riccia trichocarpa. B = optical section of apex of young thallus; x = apical cell. x 520. C = young sporeling, showing the spore and germ-tube, k; rhizoids, r; and the thallus enlarging upwards, with sunken apex, and intercellular spaces beginning to develop. x 85. (After Campbell.)

and Ferns, 1918, Figs. 27, 29, 48, 59, 76, 87, for the Bryophytes ; and for the Pteridophytes in his Figs. 149, 173, 192, 214, 258. For comparison with *Riccia* an average example of the young prothallus of a Leptosporangiate Fern is shown in Kny's drawings (Fig. 392) ; and reference to the relative literature suggests the high degree of variability presented by the early

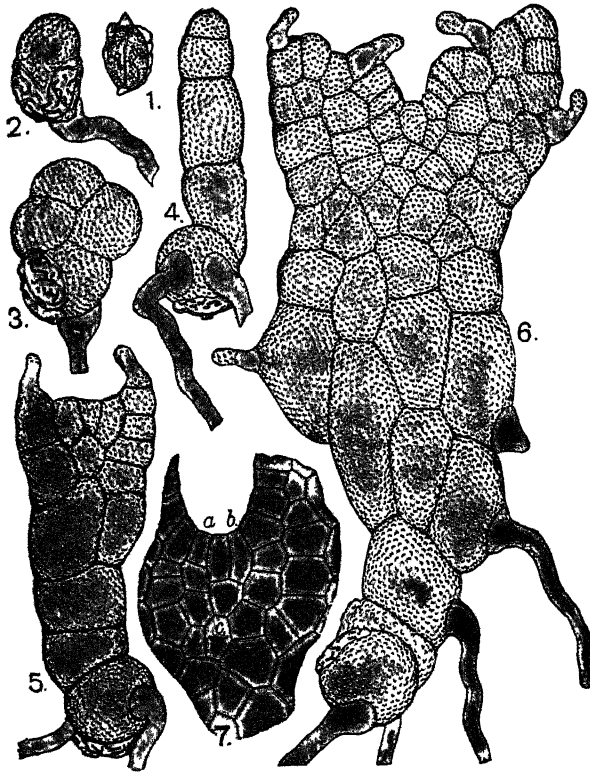


FIG. 392.
Germination of the spore and early stages of the prothallus in *Dryopteris filix-mas*.
(After Kny.)

stages of the gametophyte in both the great series of the Archegoniatae. Underlying them all, though often disguised, delayed, or even superseded, is an increase in size upwards, giving a more or less obconical form, which finds its counterpart even in the germinal filaments of *Frittschiella* (Fig. 389, 390). This is a natural consequence of photosynthetic nutrition, which brings increase of available substance in a body of primary construction ; but that physiological explanation does not discount the organographic facts. Their real interest lies in a study of the modifications of the obconical soma under varying conditions, and their final results in the form adopted by the adult haploid phase.

In Liverworts a simple filamentous but branched form appears as a brief stage (Fig. 10, p. 18); but an extensive filamentous stage is characteristic of most Mosses, and of some Ferns. Its development may be held as depending partly on inner initiative, but as being encouraged by growth under moist conditions, with low intensity of light. Experimental evidence of this has been given by Von Goebel. He used as a subject of experiment the germinating spores of *Preissia*, in which after a short filamentous stage the distal end widens normally into a flat expanse with a two-sided initial; this cell may, however, be induced under diminished light to resume the filamentous state, and the change can be repeated at will according to the conditions (Fig. 393). From such results Von Goebel suggested that if the spores were sown under

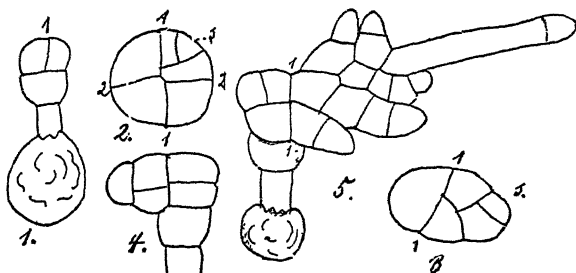


FIG. 393.

Preissia commutata, germination, semi-diagrammatic. On the short germinal tube the germinal disc forms upwards, the terminal cell usually showing quadrant-division (2). The apical cell arises from one quadrant (3); 2 and 3, present it as seen from above. (4) shows in optical section that the direction of growth of the germinal tube and the plant form a right-angle. (3) a germinal disc, seen from above, which shows how after the first division one half of the disc gives rise to the apical cell of the plant. In (5), owing to feeble illumination, the apical cell of the young thallus has grown out into a tube. (After Von Goebel.)

high intensity of light the filamentous stage might be eliminated, and the germinal disc produced at once, as it actually is in *Aneura* and *Lejeunia*.¹ On the other hand, in Mosses the result of germination takes almost always the form of a branched protonema (Fig. 48). Exceptions are most prominent in those types which are intermediate in other characters than this, e.g., *Sphagnum* (Fig. 40), *Andreaea* (Fig. 44), *Diphyscium*, and *Tetraphis* (see Chaps. IV-VI). There is, in fact, considerable diversity among Bryophytes, certain forms reacting more readily to external conditions than others. But in Mosses it has been demonstrated by Von Goebel, in *Philonotis*, that when grown in shaded water it forms large protonemal cushions without bearing any Moss-buds. Here the external conditions prolong the juvenile filamentous stage, and inhibit the more advanced state. Speaking generally the Liverworts show greater variety of form on germination than do the Mosses, the latter having almost uniformly a filamentous protonema, while the Liverworts sometimes produce filaments on germination, but more frequently cell-expanses, or massive bodies. Even that outstanding family,

¹ "Jugendformen der Pflanzen," *Sitz. K. Bayer. Acad.*, xxvi., 1896, p. 451.

the Anthocerotales, presents a like inconstancy with the thalloid Jungermanniales: sometimes a filament precedes the cell-mass (Fig. 10); or cell-division may even take place while the spore is still within the sporogonium, leading to a massive structure from the first.

In the homosporous Pteridophyta the photosynthetic prothalli also show a high degree of plasticity in their earlier stages. The ordinary cordate type of the Filicales is highly susceptible to the conditions under which it germinates. Normally a short filamentous stage precedes the flattened expanse, as in Fig. 392. But it may be extended, or indeed resumed, under diminished

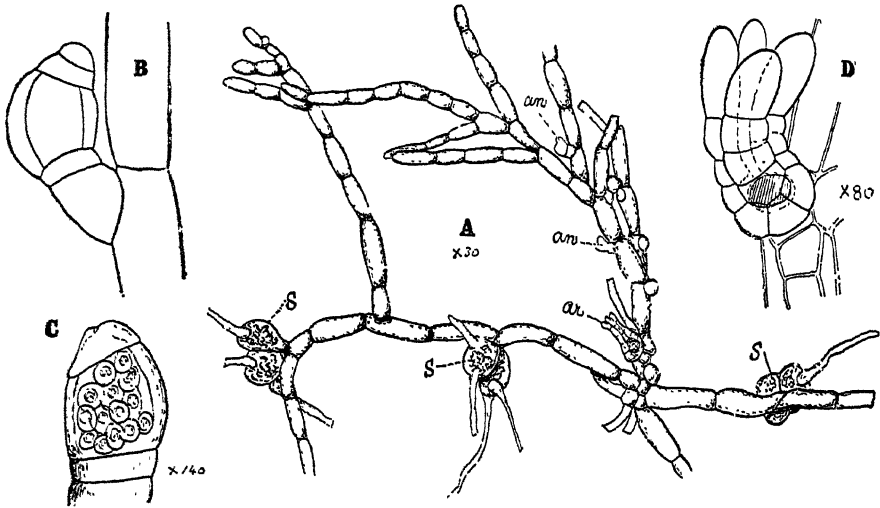


FIG. 394.

A = prothallus of *Schizaea pusilla*, bearing spherical cells (S) with endophytic fungal filaments; ar = archegonia; an = antheridia. B = segmentation of an antheridium of *Schizaea rupestris*; the lid is not always divided. C, D = mature antheridium and archegonium of *Schizaea pusilla*. (A, C, D after Britton and Taylor. B after Von Goebel.)

lighting, as it is in crowded cultures (Fig. 365). Such variability according to the conditions, the result of which has been described in Chapter XXI, compares with that already noted for *Preissia* (Fig. 393). But the filamentous state may be more fixed in certain types, as it is in *Trichomanes* (Fig. 366), or in *Schizaea* (Fig. 394). In these it is probably to be related to the peculiar biological conditions under which such plants grow.

The chief morphological interest in the gametophyte of the Archegoniatae arises, however, not so much from the initial stages of germination, and their variability according to the conditions, as from the form and structure which the more elaborate adult assumes. In point of nutrition it may be either photosynthetic, or in various degrees saprophytic. The former will be considered first. As already noted the size habitually increases upwards, giving a roughly obconical form. The principle of similarity under-

lies the conformation of the gametophyte generally in Archegoniate Plants, as it does also that of Plants at large. In accordance with it, as the size increases, if the form remains the same, the bulk increases as the cube but the surface only as the square of the linear dimensions.¹ But any deviation from the simple obconical form will in some measure meet the difficulty, by tending to maintain the due proportion of surface to bulk. Comparison of a few examples will show how in these gametophytes the difficulty of a proportionately diminishing surface is actually met by modification of the underlying obconical form.

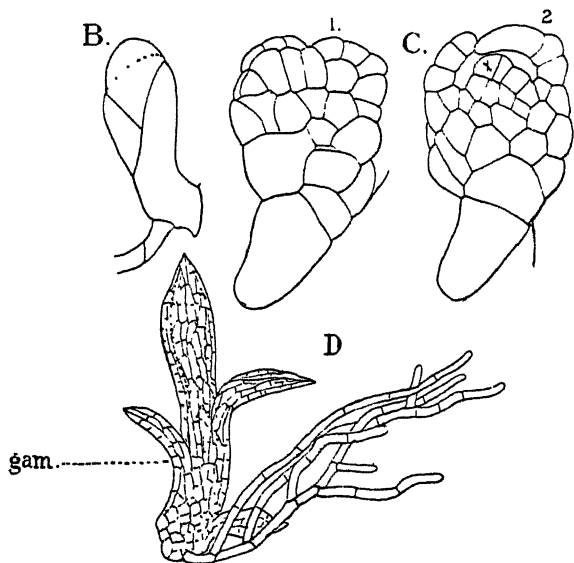


FIG. 395.

Funaria hygrometrica. B=median optical section of a protonemal bud. C=older bud (1) in surface view; (2) in optical section; x=apical cell. D=protonema with a still older "gametophore" (gam) attached. B, C $\times 225$; D $\times 36$. (After Campbell.)

In the case of the prothallus of an ordinary Fern the cylindrical germinal filament passes almost at once into the flattened expanse, with localised apical growth (Fig. 392). This flattened conical form is effective for the thallus as a photosynthetic organ, and it is shared by many Liverworts. It illustrates the simplest means of maintaining a due proportion of surface to bulk as the size increases: the thinner it is the more effective it would prove. Hence the frequency of the single cell-layer, though this is necessarily departed from when archegonia are formed. A like result follows from lobing of the thallus and finally leaf-formation, as these are seen in many Liverworts and in Mosses. The details of development of the leafy buds formed on the protonema of *Funaria*, as followed by Campbell, will illustrate this (Fig. 395). A lateral branch just below a septum of the protonema

¹ See *Size and Form in Plants*, Macmillan, 1930, chaps. i. and xii.

swells, and by intersecting walls a tetrahedral initial cell is instituted at the distal end (*B*). The first segments supply the conical base of the bud, which is at first leafless ; but each of the succeeding segments produces an imperfect foliar outgrowth (*C*, *D*). Those formed later attain the normal size and simple outline of the adult leaves. The relation of these stages to the conical expansion of the stem is shown in Fig. 395 ; it finds frequent illustration in Mosses and in the leafy Liverworts ; and this suggests that the two states, viz., the simple conical form and the leafy bud, are intimately connected with the dimensions. The plain fact is that this rudimentary type of foliar development does aid the maintenance of a due proportion of surface to bulk in an enlarging shoot. Moreover, it has a special importance where, as in most gametophytes, the shoot is composed of non-ventilated tissue.

Further, in certain Mosses the form of the leaf itself may be complicated by extension of the margin into irregular projecting teeth, or of the surface as peg-like upgrowths. But in the largest the leaf-blade may bear on its upper surface longitudinal plates consisting of chlorophyll-containing cells, which together form the chief photosynthetic system in such plants as *Catharinea*, *Polytrichum*, and *Dawsonia*. Thus by elaboration of the external surface these large Mosses are provided with a complicated, and even in some degree a controlled nutritive system, effective either for water-absorption or for gaseous interchange (Chapter V, Fig. 54). This is the extreme elaboration of surface-development seen in Mosses, and it is significant that it appears in those of the largest size.

A less regular development of lateral lobes is seen in the still more bulky conical prothalli of *Equisetum* (Fig. 146), and of the *cernuum*-type of *Lycopodium* (Fig. 200). In these again the existence of leaf-like lobes does in point of fact tend to maintain the proportion of presentation-surface of the expanding gametophyte, by an added complication of its roughly conical form. This subject will be taken up again in Chapter XXVII.

The foliar habit becomes a dominant feature in the gametophyte of the leafy Liverworts and of the Mosses : in some of them a state of specialisation appears that is comparable with that of the sporophytic leaves of Seed-Plants. Whether or not some form of demand for the maintenance of the presentation-surfaces is causally connected with the origin of such developments, there can be no doubt that this is the result of the foliar habit in the non-ventilated gametophyte. But an alternative method bringing a like result appears in certain thalloid forms as the thallus enlarges upwards ; it is brought about by the establishment of an internal ventilating system, which opens to the outside through pores of various structure (Figs. 12-15). It may be seen that this ventilation originates in relation to increasing size in the sporeling of *Riccia*. Here after a brief filamentous stage there is a rapid increase in bulk upwards, with an early establishment of apical segmentation. At first there

are no intercellular spaces ; but soon the outer cells derived from the later formed segments separate, and the characteristic air-spaces of *Riccia* are established (Fig. 391). Thus a size-relation exists for the ontogenetic establishment of internal ventilation in *Riccia*, which is biologically comparable with that of the elaboration of external form in the Moss-bud (Fig. 395). These different but cognate advances in form lie at the foundation of the two contrasted types : the *foliar* as in leafy Liverworts and Mosses by elaboration of external form ; and the *ventilated*, based upon elaboration of an internal system of spaces and stomata, as in the thalloid Liverworts. In either case the presentation-surface tends to be maintained as the size of the individual increases.

It has been described in Chapter II how in the larger types of the Marchantiales the thallus thus provided with a ventilating system differentiates its tissues, concentrating photosynthesis towards the upper surface of the flattened thallus ; how the pores may vary in structure and in detail of their origin, resulting partly from surface-depression and partly from splitting of cell-walls ; also how the several chambers may remain distinct as in *Marchantia*, or be connected, as in *Wiesnerella*, or *Plagiochasma*. There has, in fact, been a wide latitude of detail in this internal ventilation-system, which may rise to high complexity. But, conversely, comparisons carried out by Von Goebel indicate that the chambered structure may be reduced in relation to a moist habitat, and partly or wholly obliterated ; as it is seen to be in *Dumortiera* and *Monoselenium*, and in *Cyathodium*.¹ Such results following from organographic comparison prepare the way for consideration of the Anthocerotales.

In Chapter I the existence of non-functional stomata has been noted at the surface of the gametophyte of *Anthoceros*, *Dendroceros*, and *Megaceros* : they resemble structurally those that are functional on the sporogonium of *Anthoceros* ; imperfectly developed stomata have also been found on the sporogonium of *Dendroceros*, but they are absent in *Notothylas*. In the sporogonium of *Anthoceros* they communicate with an internal ventilating system, but those of the gametophyte connect only with passages choked with mucilage. Such facts taken together, and particularly the inconstancy of occurrence, appear to justify the inference of Von Goebel, that the thallus of the Anthocerotales possessed originally air-containing intercellular spaces, and that its stomata were air-stomata. Moreover, their frequent position on the lower surface of the thallus indicates that they may have been distributed all round it, as they are on the relative sporogonia. There would thus have been a far-reaching similarity between the gametophyte and the sporophyte in these relatively primitive plants. Further, the structure seen in the gametophyte of the Marchantiales points to a primitive state of ventilation for them also ; but here the structure of the stomata and air-cavities has

¹ Von Goebel, *l.c.*, p. 760.

become highly specialised in certain types, though simplified even to extinction in others, such as *Dumortiera* and *Monoselenium*. What is seen collectively in these families may be recognised as the persistent or highly modified relics of a state of a photosynthetic gametophyte, more like that commonly seen in the sporophyte than it is in any other Archegoniate Plants. This conclusion has a special significance since the most salient facts are drawn from the Anthocerotales, a group peculiarly isolated, in which both of the alternating phases are actively photosynthetic. This may probably have been the state of some, if not all of the most archaic plant-amphibians.

Thus far the description applies to gametophytes whose nutrition is chiefly or wholly photosynthetic. But in many of the most ancient Pteridophytes it may be altogether saprophytic ; or in varying degree both methods may contribute to the final result. In the Bryophytes also there appears to be some evidence of a mixed nutrition, though in them the photosynthetic preponderates. There is, in fact, no definite line of demarcation in the prothalli of the Archegoniatae as to the incidence of the two methods. In the Liverworts it appears that fungal infection is widely distributed, whether in Marchantiales or Jungermanniales, and it exists also in the Anthocerotales. But it appears to be limited to the gametophyte generation, the fungus gaining access to it habitually through the rhizoids : it is absent or rare in the region of the thallus near to a sporogonium. There is, indeed, evidence that in Liverworts a zone of tissue about the base of the young sporogonium shows immunity to infection, even leading to actual destruction of the invading hyphae, though its effect may cease after the maturity and shedding of the spores ; then hyphae may enter, but simply as parasites. In the Mosses as a whole there is practically no evidence at present of anything of the nature of mutualistic relations with fungal mycelium. The claim has, however, been made for its existence in certain specialised genera, such as *Buxbaumia* and *Tetraplodon*. In view of the dwarfed leafy plant of the former, borne on an extensive hypha-like system of rhizoids, there can be little doubt of the saprophytic nutrition ; but the question of a fungal intermediary requires to be further elucidated, though it seems improbable. Speaking generally for the Bryophyta, the relation of fungal hyphae to the tissues of the gametophyte seems, where it does occur, to be of similar biological nature to that in mycorrhiza of the vascular sporophyte.¹

Among the Pteridophytes, excepting the Equisetales, either or both of the alternating phases may be affected, and the result, or concomitant, of the symbiosis may be a modification of form of the invaded part. The prothalli thus affected are commonly of subterranean habit ; this is probably secondary, and its origin may have been, as has been suggested for the Lycopods, consequent upon the spores having been washed downwards by heavy rain into a porous loam ; or the subterranean state may have been related to such

¹ Rayner, " Mycorrhiza " *New Phyt.*, Reprint 15, chap. ix., 1927.

incidents as the fall of friable soil from an eroded bank, burying prothalli already germinated there : as was actually witnessed by Land in the case of *Angiopteris* on the Island of Tutuila, with a consequent massive cylindrical form not unlike that of certain prothalli normally subterranean.¹ (See Chapter XXI, p. 439, footnote). Such present-day happenings help to make the subterranean habit intelligible, though they offer no direct evidence of its actual source in the Psilotales, Lycopodiales, and Filicales, in all of which it normally appears. The presumption seems reasonable that a green photosynthetic habit was the original state, and the saprophytic symbiosis with an endophytic fungus derivative. Its frequent appearance in such ancient types may well have been a consequence of its possessing survival value for the plants in which it occurs. Apart from such speculations the present interest lies in the form and structure assumed under the conditions of saprophytic nutrition in plants not closely akin.

From what has been seen in *Tmesipteris* (Chap. VIII, Fig. 96), the Lycopodiales (Chap. XIV, Figs. 200, 201), and the Filicales (Chap. XXI, Figs. 367, 379), the general habit of the symbiotic prothalli has already

been indicated. It is obconical at the base, enlarging as a rule directly from the spore as a massive structure which is usually erect. It may take diverse and rather irregular form according to the conditions : a middle type for a Lycopod is suggested by that of *Lycopodium Selago* (Fig. 396). The obconical form clearly seen here is shown to be directly traceable from the spore ; and still more clearly so in *Tmesipteris* (Fig. 96). This form gives free scope to a bulky mycorrhizic development, with storage space for material saprophytically acquired. There may be a sluggish apical growth at first, and in

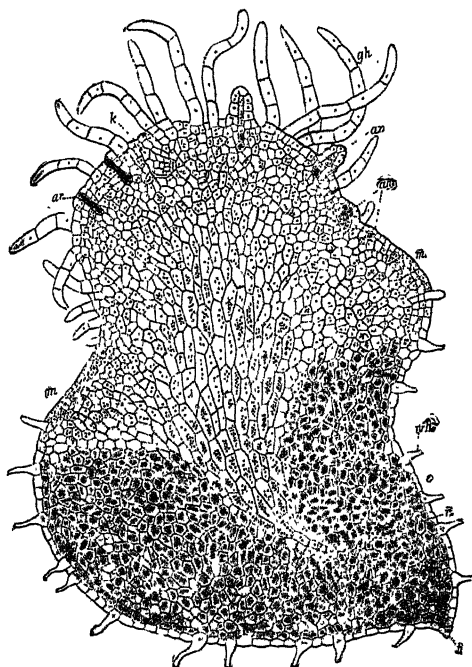


FIG. 396.

Median longitudinal section through a young prothallus of *Lycopodium Selago*. *b*=basal cell ; *nh*, rhizoids ; *e*=epidermis ; *r*=the investing tissue, stored with reserve materials, and harbouring an endophyte ; *c*=the central ; *g*=the generative tissue ; *ar*=archegonium ; *h*=young embryo ; *an*=antheridia beginning to develop ; *gh*=hairs. $\times 35$. (After Bruchmann.) The drawing shows the massive obconical thallus, with slight elaboration of form upwards.

¹ *Bot. Gaz.*, vol. 75, p. 422.

the attenuated prothalli of *Lycopodium Phlegmaria* this may be actively continued, together with branching, in accordance with the epiphytic habit of this species, which demands a wide spread (Fig. 202). But in most of the saprophytic prothalli apical growth is replaced by an intercalary meristem (*m, m*, Fig. 396), which may roughly mark off a symbiotic basal region from an upper region where the propagative organs are borne. The degree of segregation varies in different types. For instance, in *Tmesipteris* the fungal tissue may be in close relation to the antheridia and archegonia, and such segregation as there is consists merely in the absence of the fungus from the apical regions, and from the sex-organs themselves. But the distinction between fungal and non-fungal regions is specially marked in *Helminthostachys* (Fig. 367). In the *clavatum-annotinum* type of the Lycopods (Fig. 201), and in *Botrychium virginianum*, which are both subterranean, the distal end of the thallus widens out into an irregularly saucer-shaped expanse bearing the sex-organs either marginally or superficially. But in the type of *L. cernuum* (Fig. 200), where the distal region is sub-aerial and photosynthetic, the well-known lobes are formed, about the bases of which the sex-organs are borne. In upright cylindrical prothalli such as are seen in *Tmesipteris* and *Psilotum* (Fig. 97), in *Ophioglossum vulgatum* (Fig. 379), and in *Helminthostachys*, the antheridia and archegonia are distributed equally all round the cylinder, and are commonly intermixed. This shows a rudimentary state of organisation, with radial symmetry. Even in the *clavatum* and *cernuum* types of *Lycopodium* there is little precision in the place which the sex-organs respectively take upon it. The general conclusion to be derived from such comparisons in the prothalli of plants of very different affinity is that, whatever the minor deviations of form, *the construction is fundamentally radial*; that apical growth is not a marked feature; that, though appendages may exist, they suggest local enation rather than the formation of specific appendages; and that the position of the sex-organs is not defined. In fact, that the whole organisation, apart from the symbiotic relation, is on a low level, readily dominated by the conditions, and particularly by the influence of the invading fungus; and that there is a marked tendency towards tuberous development.

These saprophytic prothalli are all massive structures, consisting wholly of parenchymatous tissue. A peculiar feature is that notwithstanding their great bulk the tissue is without any obvious source of ventilation by intercellular spaces. The drawings of Treub, Bruchmann, Jeffrey, Lawson, Lang, and Holloway give unanimous evidence that they are, like most other gametophytes, unventilated. Nevertheless, the contours of these large prothalli are simple, and the presentation area of external surface is not maintained by complication of form as they increase in size, except in a minor degree by occasional branching, or by the formation of leaf-like lobes as in *L. cernuum*. Among the largest of such prothalli known are those of *Botrychium virginianum*, which may live for several years; when old they may attain a length of 20 mm., with a breadth of about 15 mm., but with no further complication

of outline than relatively slight irregularity. Such facts as these contrast strongly with that great range of modification, either of external form or of internal ventilation, which tends in plants at large to maintain a due proportion of surface to bulk. Here there is no formal or structural change as the size increases. In fact, these prothalli appear as a prominent exception to that correlative adjustment of Size and Form that rules generally in vegetation, but especially among sub-aerial plants.

In her comprehensive and critical Essay on "Mycorrhiza" ¹ Dr. Rayner refers to the work of E. V. Laing on Tree-Roots (1923), in which he points to the presence of large amounts of oxidising enzymes in the mycorrhiza of trees, and discusses the possible advantage of this increased oxidising mechanism to the trees, in habitats of deficient aeration. It seems possible that a similar resolution of the physiological difficulty which would follow from the apparent structure may serve as an offset in these bulky prothalli. Hitherto there is no direct evidence of the existence of oxidases in the prothalli; hence the present position must be one of suspended judgment; but with the *proviso* that the existence of the unventilated prothalli must not be held as opposing the principle so amply demonstrated elsewhere, until it is proved that no such oxidising agency exists in these sluggish, saprophytic prothalli. The only alternative source of oxygen would appear to be by slow diffusion in the liquid in which the tissues are bathed.

GAMETANGIA

Examples of the gametangia of the Archegoniatae have been described and illustrated in the preceding Chapters; and references have been given to works in which the results of their more detailed study have been set down. The material is thus afforded for some general comparison. It cannot be assumed that they have all originated from a common source. Here as elsewhere homoplasy may have played its part in their evolution, and such similarity as they show in plants of varied conformation may have been determined in part, and possibly in essential features, by the circumstances under which they were evolved. Any decision as to the degree to which this is so can only be attained by induction based upon wide comparison. Such ideas should form a background to all formal treatment of the gametangia of the Archegoniatae. Comparison of antheridium with antheridium, and archegonium with archegonium in the several genera, families, or classes is only one phase of the organographic problem. Beyond this lies the comparison of the two types of gametangium, that is between antheridia and archegonia; and, finally, between gametangia and sporangia, as diverse stages in the same individual life. The wider the net of such comparisons is cast the greater should be the care to distinguish between homoplastic similarity and that of true relationship by Descent. Doubtless these remarks will be read as platitudes of evolutionary study. The reason for their statement here is

¹ *New Phyt.*, Reprint No. 15, 1927, p. 135.

that these propagative organs being themselves more constant features in each life-cycle than the vegetative organs that bear them, their characters must take the premier place. At the moment we shall consider the comparisons first named, and leave over the discussion of such likeness as exists between gametangia and sporangia to Chapter XXIX.

The gametangia of the Archegoniatae differ from those of the Thallophytes in possessing an external wall of sterile cells, the biological importance of which in sub-aerial life requires no explanation. They may be sunk

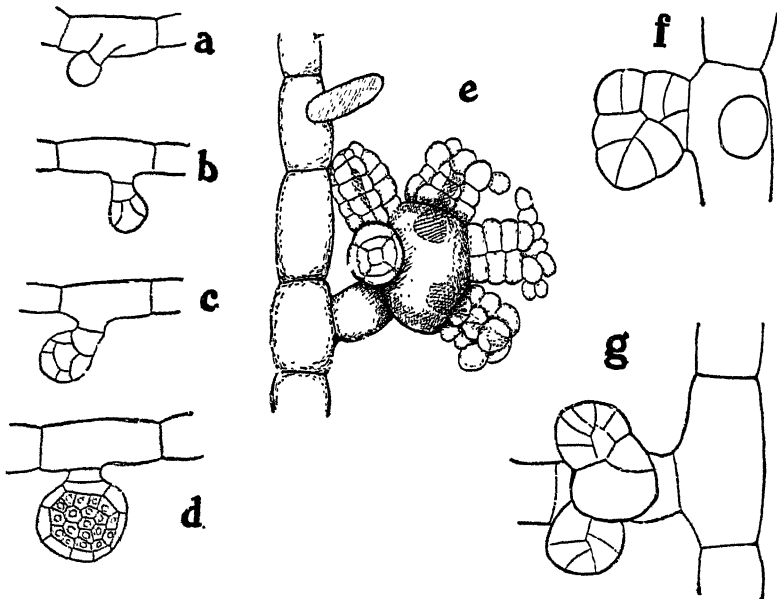


FIG. 397.

Trichomanes pyxidiferum. a-d=development of an antheridium; e=archegoniophore, with five archegonia; f, g=development of an archegoniophore. $\times 150$.

in the tissue of the gametophyte, or they may project from it; sometimes they are even borne distally on simple filaments. In the former case the wall is not specifically developed as such, the protection being carried out by the surrounding cells of the thallus; but the distal end is always covered in by protective cells, some of which may be specialised as an opening mechanism. Where the gametangia project the cells of the wall form a complete covering. This protection holds equally for antheridia and archegonia. In the former a compact mass of spermatocytes within produces from each cell a single motile sperm: in the latter there is normally present one central row of cells, of which the upper part forms a varying number of transitory canal-cells, while the basal cell, after division to form a ventral-canal-cell, becomes the solitary egg. These last features are constant for the Archegoniatae. Of their two Divisions the gametangia of the Pteridophytes are the more highly

standardised, and they will be taken first. The variants which they show consist chiefly in the degree to which they are embedded in the tissue of the thallus. In the more highly specialised Pteridophytes, particularly where the vegetative region that bears them is filamentous, as in the Schizaeaceae or the Hymenophyllaceae, both types of gametangia project: an antheridium may even be borne distally on an attenuated filament (Fig. 365); but the archegonia are always borne on a massive archegoniophore, with the venter protected or even immersed, while the neck projects (Fig. 397). Both, however, conform in the essential features of structure and development to the

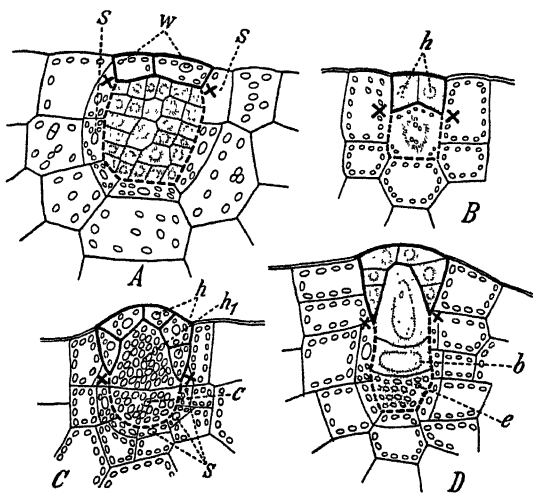


FIG. 398.

Antheridia (A and B) and archegonia (C and D) of Marattiaceae in longitudinal section, diagrammatised after Jonkmans' drawings, from Von Goebel. The cover cell with its derivatives are drawn in heavier lines, and the lower limit marked *x*. The inner cell is shaded. B=a younger stage of development common for both.

type seen in the Marattiaceae, where the gametangia are deeply sunk. Early stages in the development of the antheridium and the archegonium in these relatively primitive Ferns are shown slightly diagrammatised in Fig. 398. Each of these organs originates from a single superficial cell, and (B) suggests this for both. This cell undergoes periclinal cleavage, by walls marked *x*, *x*. The outer cell, after further division, gives rise in the antheridium to the multicellular "lid," with its opening mechanism; the inner, after repeated cleavages, forms the numerous cubical spermatocytes (A). In the archegonium the inner cell undergoes fewer cleavages: the first, which is periclinal, separates an outer canal-cell (C, *h*₁) from an inner cell (C, *c*); this by a second periclinal division gives rise to the ventral-canal-cell (D, *b*), and below it to the egg (D, *e*). The egg, ventral-canal-cell and canal-cell form the central series; and it may be held that this corresponds by position and by origin to the whole block of the spermatocytes in the antheridium.

But in the archegonium the cleavages are simplified in accordance with the fact that only a single female gamete is functional. Meanwhile crosswise cleavages have divided the outer cell (*B*, *h*) into a rosette of four; and in each of these repeated parallel cleavages may produce four rows of cells which constitute the neck of the archegonium: this may be held as the correlative of the "lid" of the antheridium. Thus it is possible to compare the two types of gametangia of the same organism, and see that beneath their differences of adult structure and of function there is an underlying similarity of development.

On the other hand, in *Lycopodium*, while the antheridia are sunk in the tissue of the thallus as before, the archegonia project more definitely from the prothallial surface (Fig. 205, *B*, p. 263). The neck consists, as in the Ferns,

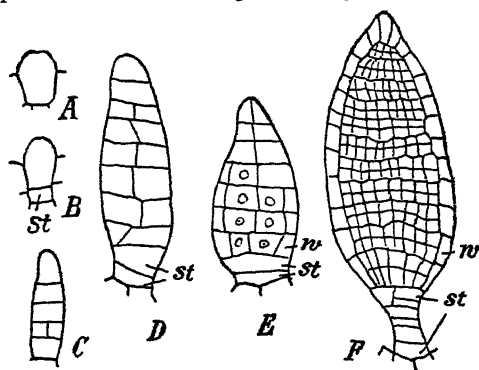


FIG. 399.

Stages of development of the antheridium in *Fegatella*. (After Bolleter, from Von Goebel. *Organographie*, 3rd Ed., p. 145. For description see text.)

of four rows of cells, but each results from more numerous cleavages than in the Marattiaceae, while the central series here consists of some half-dozen or more canal-cells. The antheridia of Lycopods, however, resemble those of the Marattiaceae (Fig. 205, *A*). Further, reference may be made to Figs. 98, 99, which represent the gametangia of *Tmesipteris*. In this very ancient type the sex-organs conform to those of other early

Palaeozoic stocks, such as the Lycopods and the Eusporangiate Ferns. The conclusion follows that the gametangia of the most primitive Vascular Plants now living are essentially alike in construction: that they are commonly sunk in the tissue of the thallus, and that, though differing in detail according to sex, the antheridia and archegonia conform to a common type of origin which ensures the protection of the gametes up to the time of maturity.

The gametangia of the Liverworts, notwithstanding an apparent diversity related to the various ways in which they are disposed, may also be shown to share a common type of structure, by comparisons based rather on the initial segmentations than upon their mature form.¹ The antheridia appear here as elsewhere to retain the original character rather than the archegonia, and those of the Marchantiaceae may be taken as a primitive type. The adult is club-shaped and shortly stalked, with a single-layered wall covering a mass of spermatocytes within. It arises from a single cell,

¹ See Von Goebel, *Organographie I.*, p. 145, etc.

which elongates and divides by successive transverse cleavages to form a row of disc-shaped cells: each of these divides by intersecting radial walls, first into halves, then into quadrants. This is followed by a periclinal cleavage in each, the inner cell subdividing to form spermatocytes, the outer forming part of the wall (Figs. 399, 400, I). The antheridia of the Jungermanniaceae appear as a result of modification of this type: first, a reduction is seen in the smaller number of the discs that compose it, usually only one of these being fertile; and, secondly, in a change of the subdivision of the disc. It is halved as before (Fig. 400, II, 1, 1); but this cleavage is followed in each of the resulting cells by a wall inserted upon it at an angle of 45° (2, 2), and later a periclinal wall follows (3, 3). Thus the disc is divided into two inner fertile cells,

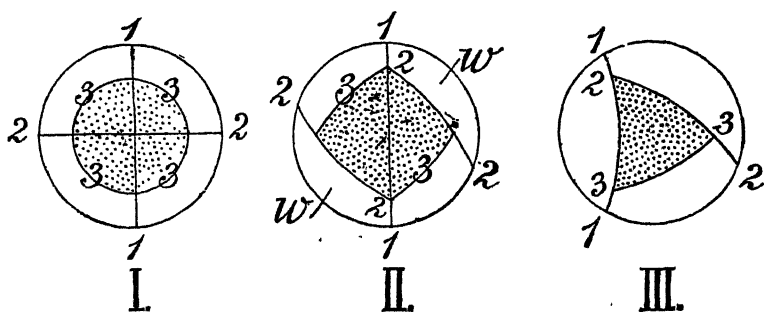


FIG. 400.

Diagrammatic transverse sections: I.=through an antheridium of the Marchantiaceae; II.=of the Jungermanniaceae; III.=of a Liverwort archegonium. The fertile cells are dotted. *w*=the sterile wall-quadrants. (After Von Goebel.)

and four cells of the wall. This is important for comparison with the segmentation of the archegonium of Liverworts generally: but in their development the reduction goes a step further than in the antheridium of the Jungermanniaceae. Comparison of its cleavages indicates that an archegonium corresponds only to one half of such an antheridium, in the sense that one half is sterile and contributes only to the protective wall, while the other half is fertile, the cleavages in the disc that gives rise to it being comparable to those in the antheridium (Fig. 400, III). The development of the archegonium of a Liverwort from a single parent cell has long been known, with the cleavages as in Fig. 401. But now it may be interpreted in terms of the antheridial structure, as suggested in Fig. 401. A transverse wall separates the stalk from the immediate mother-cell. This undergoes segmentation by three longitudinal walls corresponding to those of Fig. 400, III. The result is one central fertile cell surrounded by three sterile cells (Fig. 401, 1, 2). The fertile cell at the centre then divides transversely, and the outer cell forms the "lid," giving rise to the distal rosette of cover-cells, the inner forming the central series. The cover-cells are then raised on the elongated neck of the archegonium, which is formed from the upper half of the three lateral

sterile cells, while the lower halves of them form the ventral wall. Meanwhile the inner fertile cell undergoes further transverse division to give the canal-cells (h), while the lower part produces the ventral-canal-cell, and the egg (c_1).

This view of the archegonium of a Liverwort as the equivalent of a fertile half of an antheridium of the type represented in section in Fig. 400, II, has been supported by Von Goebel by actual observation of the young archegonia of *Makinoa crispata*, in which he found the structure variable to such a degree as to suggest intermediate conditions between antheridia and archegonia: these states were due to the fact that not only one fertile cell was present, but two or even four. This shows in young archegonia of *Makinoa*

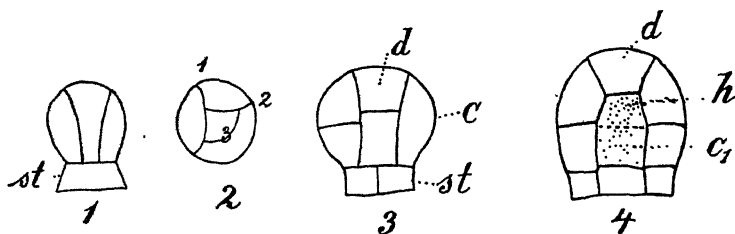


FIG. 401.

Diagram of archegonial development in the Liverworts. 1, 3, 4, in longitudinal section; 2, in transverse section—corresponding to Fig. 400, III. In 3 the inner cell is separated from the cap-cell. In 4 the fertile cells (h and c_1) are dotted. st =stalk. (After Von Goebel.)

a near approach to quadrant-development, as seen in the antheridium.¹ Following upon these comparisons of the cleavages in development of the antheridia and archegonia of Liverworts it may be concluded that, as in Ferns, the two types of gametangia are referable to a common source, and are, in fact, homologous; but differentiated in relation to sex.

The gametangia of the Mosses show essential likeness to those of the Liverworts, but they project more freely from the surface of the plant; and they differ in some details, particularly in their segmentation. The antheridia are initiated as before from a single cell, which segments transversely at first, but later a two-sided initial cell is established with alternating segments (Fig. 58, Chap. V). Otherwise the analogies are close, excepting that the distal pore of dehiscence is more highly organised. The mode of segmentation is not, however, a distinctive feature for Mosses only: it occurs in the Liverwort, *Monoselenium*. The further internal cleavages are as in the Jungermanniaceae; and so, as Von Goebel remarks, the Moss antheridium bears in a manner a combination of the characters of the Marchantiaceae and the Jungermanniaceae. The development of the Moss archegonium has been described in Chapter V, p. 82, and the conclusion has been

¹ For the full argument, and figures and references, see Von Goebel, *Organographie*, 1928, part i., p. 147.

adopted that, notwithstanding the formation of an elongated neck as a consequence of the repetition of the simpler segmentation of the Liverwort archegonium, it may be referred to the same fundamental type as these (Fig. 59). An exception is, however, seen in the Sphagnales (Chapter IV, Figs. 41, 42), which take in respect of the segmentation of their gametangia a middle place between Liverworts and Mosses. Such facts are cumulative in showing that the two Classes are cognate rather than sharply distinct. Even the Anthocerotales, with their deeply-sunk archegonia and endogenous antheridia, conform in the detail of segmentation to that of some generalised type which would include all Liverworts (Chap. I).

A striking feature which all of these gametangia have in common is the constancy in character and relation of their contents: indeed the central series of the archegonium is almost as fully standardised in the Archegoniatae as the contents of the embryo-sac are in Angiosperms. The number of spermatocytes and of the canal-cells may vary, as also the number and in some measure the position of the cleavages by which they and the protective walls are produced; nevertheless the gametangia do show such a degree of uniformity that they give a safe foundation for comparative argument. Both in Bryophytes and Pteridophytes the similarity of the developmental steps in antheridia and archegonia points to a common origin from a type of gametangium resembling that of the antheridium. Here again, as in the differentiation of megasporangia and microsporangia, the male is conservative of ancient character, while the female diverges by changes of detail readily recognised as adaptive in relation to the receptive and nursing functions.

The conclusion drawn from such comparisons has led various writers to homologise the primitive undifferentiated gametangium with that of some Algal ancestor. The argument based on comparison with the Phaeophyceae was first stated by B. M. Davis,¹ and illustrated by diagrams here quoted as Fig. 402. It is easy to place in series the gametangia of certain Algae and those of simple Archegoniates, and to trace theoretically the origin of the latter from the former by steps of added complexity, involving in particular the origin of a protective wall, so essential a feature in the life of land-plants. But the actual production of the wall has not been proved comparatively moreover, it is still an open question whether the nearest points of phyletic contact of the Archegoniatae with any Algae are to be found in the Red, the Brown, or the Green Algae of the present day. So long as no actual intermediate types between Algae and Archegoniatae are at hand these comparisons bear the mark of aspiration rather than of any definite conclusion. The question may fitly be left at the point that probably there was for the Archegoniatae some general and undifferentiated original type of gametangium, such as is prefigured by various Algae, and that its function was to produce many motile gametes.

¹ *Ann. of Bot.*, xvii. p. 477.

Notwithstanding that degree of self-protection of the gametangia afforded by the sterile wall, they and the embryos within must have become increasingly vulnerable as the plants that bore them advanced towards a full sub-aerial habit. The danger has been met by various protective measures. The simplest is that of sinking them into the tissue of the massive thallus, as in such primitive types as the Anthocerotales, Psilotales, Lycopodiales, and the Eusporangiate Ferns. But in those Bryophyta in which the sexual organs project protection is secured by other means: in this the antheridia are less favoured than the archegonia. The protection is often by

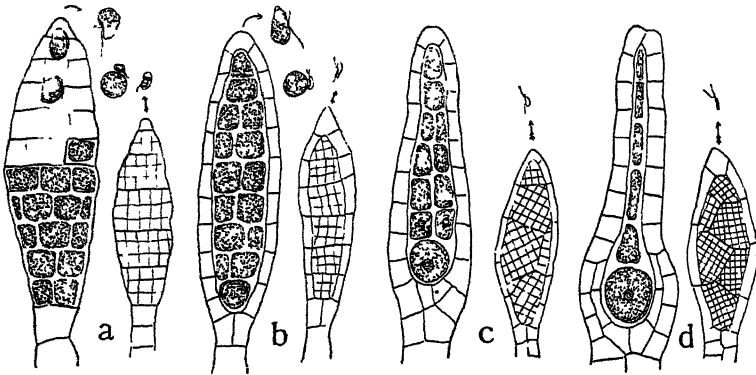


FIG. 402.

Diagrams illustrating the possible evolution of the archegonium and antheridium from the plurilocular sporangium. *a*=plurilocular sporangia with large and small gametes discharged from the apex, after the habit found in certain Phaeophyceae. *b*=plurilocular gametangia of a hypothetical algal type, which has adopted a terrestrial habit. The outer layer of gamete-mother-cells has become sterilised as a protective capsule enclosing the fertile tissue. The gametes are differentiated in sex, but both motile. *c*=plurilocular gametangia of somewhat higher hypothetical forms. Stenosylation has proceeded so far in the female that only a few eggs are matured at the base. *d*=simple types of archegonium and antheridium: the female gametes reduced to one, while the number of the male gametes is greatly increased, and these cells are smaller and more highly specialised. (After B. M. Davis.)

individual shielding by leaves, or by massing them together with paraphyses and specialised perichaetial leaves. But the archegonia are often more carefully protected, especially in the Liverworts; here not only may each archegonium be surrounded by its own perianth but a perichaetial curtain may envelop a group of them, as in the Marchantiaceae, where it is specially necessary: for there they are borne up on the erect archegoniophores as the sporogonia develop. A still more effective protection is seen in various Jungermanniales which have adopted a marsupial habit (see Chapter III, p. 54). With these and other detailed features a general tendency is seen in the more advanced types both of Liverworts and Mosses to segregate the vegetative from the propagative organs, and also to separate the sexes. Advances in this respect are homoplastic in the two Classes: they present analogies with what appears in the vascular sporophyte, with its vegetative organs and sporangia. In the Liverworts and Mosses this segregation of

vegetative from propagative regions marks the highest point of organisation reached by the gametophyte of land-living plants. In the haploid phase of the Pteridophytes there is a like tendency to segregate the sexual organs, but this together with the form of the vegetative system plays within narrower limits.

The most general underlying feature of the gametophyte in Archegoniate Plants is the obconical form. It appears with strongly marked radial symmetry in *Tmesipteris* (Fig. 96), the Ophioglossaceae (Figs. 367, 379), and the Lycopodiaceae (Figs. 201, 204). There is a tendency to dorsiventrality in *Equisetum* (Fig. 146), which is more pronounced in the cordate type of the Filicales; but even this may be held as an inverted cone with dorsiventrality imposed upon it. It has been shown repeatedly in the Leptosporangiate Ferns, as well as in *Angiopteris*, how there may be a transition under special conditions from the cordate to a cylindrical form (Fig. 368). It seems legitimate to look upon such a state as a throw-back to a primitive cone or cylinder, such as is normally present in *Helminthostachys* or in *Ophioglossum*. Such forms as these, occurring among the earliest Eusporangiate types, and coupled with the prevalent obconical prothalli of the Lycopodiales and Psilotales, suggest that a primitively erect, conical or cylindrical gametophyte was a common feature in early Pteridophytes. From this by plagiotropic development, by occasional formation of irregular leaf-lobes, and by reversion in certain cases to a filamentous form, the types of gametophyte now usual in the Filicales would have arisen. On the other hand, in some a tuberous development has accompanied a mycorrhizic synthesis, while epiphytic saprophytism has led to its widely branched and attenuated form in *Lycopodium Phlegmaria*. Thus the haploid phase of the Pteridophyta possesses some degree of plasticity. But its morphology has played within narrow limits of change. Accordingly the prothallus takes only a secondary place in the systematic comparison of Vascular Plants.

The comparisons contained in the preceding paragraphs make it possible to form some idea of the nature of the gametophyte in those early denizens of the land which gave rise to the living Archegoniatae. Though doubtless the ultimate origin may have been filamentous, comparison suggests that this simple construction was not maintained by the earliest colonists. These probably adopted a robust build, not only of their gametangia, with their protective wall of cells, but also of the haploid vegetative phase that produced them. The gametangia may even have been at an early stage sunk in its tissue, as they are seen to be in the Lycopods, the Eusporangiate Ferns, and Psilotales, as well as in the Anthocerotales. There is no reason to assume that the evolution was monophyletic: it seems more probable that it resulted from progressions along a plurality of lines. Be this as it may, the divergence must have occurred early which gave origin to the Bryophytes with their dominant gametophyte, and to the Pteridophytes with their dominant sporophyte. Of

the more primitive living Archegoniatae it seems probable that the Anthocerotales take a special place as a synthetic type : chiefly on the ground of the absence of appendages, the imperfect segregation of nutritive and propagative regions, and the similarity of the two alternating phases. Comparison indicates progressive segregation and specialisation of the nutritive and propagative parts in the Bryophyta, with its highest results respectively in the Marchantiales, the higher Jungermanniales, and the largest of the Bryales ; while the Sphagnales take a significantly intermediate place. With the appearance of such types the progress of the gametophyte stops. The haploid phase was structurally doomed to be no more than a partial success, as a land-living organism : for it never fully combined the elaboration of external form with the advantage of internal ventilation, though both were achieved by it separately.

CHAPTER XXVI

EMBRYOLOGY ¹

THE high degree of standardisation seen in the archegonium of Bryophytes and Pteridophytes, and particularly in its central series of cells, concentrates upon the single, deeply-seated ovum. Occasionally two eggs may be present ; such happenings may perhaps reflect back to a time when a plurality of ova were present in a single gametangium of an algal type. But normally in all Archegoniatae there is only one egg. From it the sporophyte arises : and the first stages of development of the embryo are carried out *in situ*, with the tissue of the gametophyte as a closely applied protective and nutritive nurse. The period of gestation varies, and the details of the continued relation of embryo and parent are not uniform for the Archegoniatae. But the general scheme is the same for all. It involves a co-operation of the two phases of the life-cycle which is believed to have originated in relation to amphibial life. But, whatever the history of its origin, the biological importance of this internal embryology for land-living plants may be estimated from the constancy of its recurrence in all Archegoniate Plants. It is to the early stages of the encapsulated sporophyte that the term " embryo " is usually assigned.

There is an obvious analogy in respect of internal gestation between the two Kingdoms of living things, which has a natural foundation in the vulnerability of the primordial cell against the risks of sub-aerial life. As Weismann remarked in 1882, " The birthplace of all animal and plant life lay in the sea." In the earlier submerged stages, whether of animals or of plants, the gametes could safely be voided into water ; and not only syngamy but also germination could be effectively carried out there. It is believed that for both Kingdoms sub-aerial life was derivative. The course of their evolution was diverse ; but the step to dry land brought to both similar risks : in particular those of desiccation, and of mechanical damage to the primordial ovum, and to the early stages leading to the adult individual. There must always have been the question of nutrition ; but in this the stress of circumstance will have been much more severe upon the predacious animal than on the self-nourishing plant. An indication of this appears in the fact that internal gestation appears in certain Elasmobranch and Teleostean Fishes, while it is habitually absent in the Algae. Nevertheless, for both Kingdoms the sum of factors favouring internal gestation in sub-aerial life must have been decisive. The proof that it was so is found in the prevalence of the habit in the higher terms of both Kingdoms.

¹ This chapter is based upon an Opening Address given as President of the Royal Society of Edinburgh, October, 1922.

The facts as known in the Animal Kingdom are suggestive in relation to Plants: in particular, it appears that the habit has been polyphyletic in its origin in Animals. In the Elasmobranch and Teleostean Fishes it presents various detail, and is undoubtedly of independent origin. It recurs independently also within the circle of the Amphibians. It is found again in certain Marsupials; but it is in the typical Mammals that the habit has become a confirmed feature. The conclusion will be that internal gestation has originated at many distinct points among vertebrate Animals, and that since it is seen in certain Fishes it is not exclusively referable in origin to sub-aerial life, though this has doubtless tended to establish it in the Mammals. Further, in Animals, with a few rare exceptions, *e.g.*, in certain Teleostean Fishes, the ovum does not develop *in situ*: it is extruded from the point of origin, and fixes itself secondarily upon some convenient internal spot, which is not identically the same even in organisms related to one another. In Plants—excepting the peculiar post-syngamic conditions seen in the Rhodophyceae and in certain Fungi—the internal gestation follows a more stable plan. The ovum is not discharged, but is fertilised *in situ*, and the development of the embryo follows in the venter of the archegonium: these facts are related to the high stabilisation of its structure. On the other hand, the strong contrast between the external germination of most Thallophytes and the internal gestation present in all of the Archegoniatae leads to a theoretical correlation between the alternation as seen in the Archegoniatae and the spread of vegetation from the water to the land. The protection of the defenceless zygote appears as a feature adaptive to sub-aerial life. Nevertheless, the facts derived from the Animal Kingdom suggest, first, that a land-habit is not necessarily the only determining condition of internal gestation; and, secondly, that the response has been polyphyletic for them, though this question may remain an open one for Archegoniate Plants.

In 1909 Dr. W. H. Lang suggested that the problem of alternation as seen in the Archegoniate Plants is one of ontogeny as well as of phylogeny; hitherto the latter aspect had chiefly claimed attention. That the development of the individual from the germ is liable to be influenced by the conditions. That in the case of the zygote of an Archegoniate an important factor may well have been its relation to the enclosing prothallus; and the difference between this and the free germination of the spore may account in some measure for the difference of form seen between the haplophase and the diplophase in Archegoniate Plants. Moreover, the retention of the egg in the venter of the archegonium would fit well biologically with the departure of the organism from aquatic life, and in so far it would accord with the correlation of archegoniate alternation and the establishment of a land flora. But this does not decide the question of origin of the diploid phase. It may have been existent in the ancestry as an independent soma, prior to establishment on land; and the presence of the embryo in the venter be due to retention *ab ovo* of a phase originally free. There is, however, no comparative evidence derived from organisms of near affinity to support such a suggestion, and a reply to the question (essentially an "academic" one till decisive facts are available) must rest upon a balance of probabilities rather than on demonstration.¹

¹ *New Phytologist*, vol. viii., p. 104.

POLARITY AND THE PRIMITIVE SPINDLE

The behaviour of Algae in establishing new individuals provides material for comparison with the higher land-living plants. In planktonic Algae the young cells commonly round off to a spherical form, and in the smaller types this is not departed from: the sphere and the disc are forms convenient for plants of floating habit, a state which demands no distinction of apex and base. But where, as in benthic organisms, the plant is related to a solid substratum, *polarity* is established, and with it follows as a rule an elongation of the plant-body into a *cylindrical or spindle-like form, with a distinction of apex and base*. The simplest type of this is seen in the non-septate filament of the Siphoneae. But in the vast majority of Algae the plant becomes septate, so as to form a single filamentous row of cells. This is seen in various green, brown, and red Algae (Fig. 403). The simple filament may be retained throughout life, as in *Ulothrix* or *Chaetomorpha*; but usually it is branched (Fig. 403, iii), and this leads on to those various forms of aggregation of filaments which constitute the somata of many Algae, and of the Fungi generally.

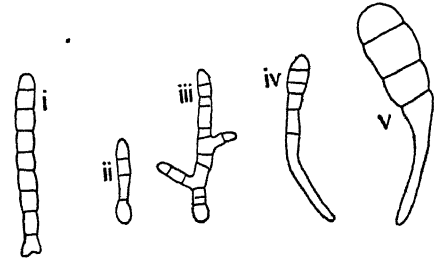


FIG. 403.

Germinating spores of Algae. i, *Ulva*; ii, iii, *Asperococcus*; iv, *Cutleria*; v, *Callithamnion*. (All after Bornet and Thuret.)

A further modification, and one which is more important in relation to the higher forms of vegetation, is the subdivision of the cells of the simple filament by longitudinal walls, the result of which is either a bilaterally flattened or a solid cylindrical structure. In most Algae this longitudinal cleavage of cells does not begin until the filament is established, and it appears towards the distal region of it. Where the plant-body takes an obconical form, tailing off below to a simple filament, the basal attachment may often be strengthened later by accessory growths. This form is seen in *Laminaria*, or in *Fucus* (Fig. 404). In the latter the filament is short and unbranched; consequently the young thallus appears as the direct product of the germinal filament. Illustrations of this may be drawn from various types of Algae, and from either the diploid or the haploid generation. Oltmanns specially remarks that in the Rhodophyceae there is no difference between the germination of carpospores and tetraspores. Such germinations may all be held as embodying solutions of the same basic problem, viz., the establishment of a new photosynthetic individual in a uniform medium, but with attachment to a solid substratum, the surface of which faces towards a source of light.

Such familiar facts as those above quoted should be borne in mind when discussing the embryology of the higher forms of vegetation. It is true that they hardly come under the term "embryology" as used in the restricted sense that the young individual is enclosed within the body of the mother. But it cannot be denied that the embryo of the Archegoniatae and of Seed-Plants represents a young individual with requirements cognate to those of some Algae, though encapsulated in the archegonium in accordance with life on exposed land-surfaces. Such comparisons should not only be in respect of form, but also of biological condition.¹

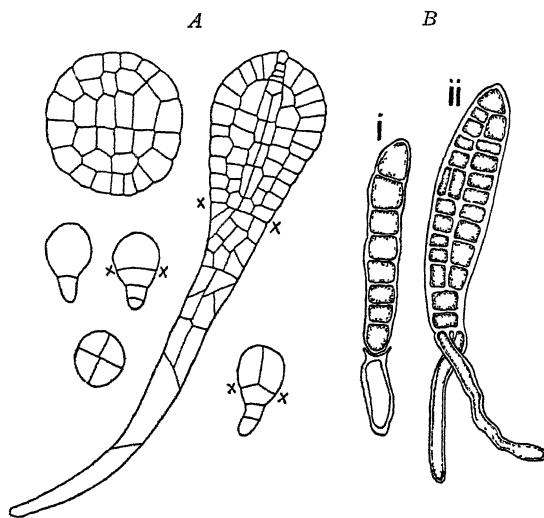


FIG. 404.

A, embryos of *Fucus*. (After Rostafinsky.) x, x=Rostafinsky's "Grenz wand."
B, young sporophytes of *Laminaria digitata*. (After Klyn.) i \times 322. ii \times 390.

The chief differences of condition of the embryo encapsulated in an archegonium from the free sporeling of an Alga lie in the absence of direct relation to a solid substratum, and in the substitution of the nutritive medium by the living tissues of the gametophyte. The incidence of gravity remains effective, and of light also where the embryology is not subterranean, though its effect will be diminished by having to traverse the enveloping tissues. Of these factors the strongest influence upon the earlier stages of the embryo lies in the enveloping maternal tissue. This may be ascribed not only to the cells immediately adjoining the embryo, but also to the direction in which the chief bulk of the gametophyte tissue lies, from which the nourishment of the embryo is to be derived. In point of fact, the uniform nourishing medium surrounding the free Algal germ has been substituted by a nourishing tissue

¹ See Lang, "Discussion on Alternation," *New Phyt.*, vol. viii., p. 104. Address to Sec. K Brit. Association, Report, 1915, Manchester.

which, as a rule, is not uniform in bulk on all sides. It may accordingly be anticipated that though a cylindrical or spindle-like form of the embryo is possible, this will not be constant, or permanently retained.

In all Archegoniate plants a definition of the polarity of the embryo is the first step in its development. The position of its *apex* and *base* is recognisable on the appearance of the first segmental wall. This is itself defined by the position of the first nuclear figure. What, then, determines the position of the nuclear figure? The nucleus of the zygote often occupies a central position in the egg: this is especially so where the embryo is at first spherical in form. But in cases where a suspensor is to be formed, the nucleus may approach the apical end of the elongating zygote.¹ In animal ova where there are considerable masses of yolk, and the greater part of the cytoplasm lies at one pole, the nucleus lies at the centre of the mass of cytoplasm, and the first cleavage divides the cytoplasm about equally into two daughter-cells. But it has been found that by pressure between glass plates, or by sucking an ovum into a tube of diameter narrower than that of the egg, the first and even the succeeding divisions can be so controlled that repeated cleavages appear in planes including the direction of the pressure.² Kny has obtained similar results by experiments on the ova of

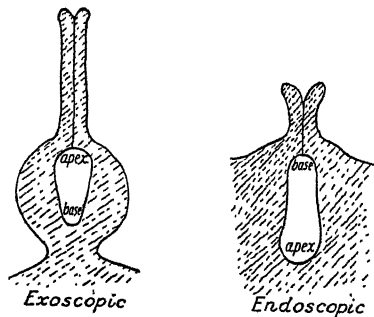


FIG. 405.

Diagrams illustrating the two main types of polarity of the embryo in Archegoniate plants.

Fucus, and on the germinating spores of Pteridophytes.³ These observations may probably present a real parallel to what is seen in many Archegoniatae. In both cases a spindle-shaped embryo results, made up of a row of cells. The facts suggest that pressure exercised by the surrounding maternal tissues may have a direct effect in Archegoniate plants. The archegonium with its neck is in fact a tube open at one end, and more or less distended below. If it acted in the way suggested, exerting a lateral pressure on the developing embryo, the axis of the embryo would then coincide with that of the archegonium. As a matter of fact, it does so coincide in the great majority of Archegoniate plants, though not in all. But this simple explanation could not account for the definition of the polarity seen in Angiosperms, where the zygote projects freely into the semi-fluid contents of the embryo-sac: nor could it apply in the case of the free-living Algae. Pressure may be one factor; but among others that may also have

¹ Compare *Land Flora*, Figs. 262, 266 (=Fig. 382 above).

² Przibram, quoted by Doncaster, *Cytology*, p. 40.

³ *Jahr. f. wiss. Bot.*, Bd. xxxvii., 1901, pp. 69, 96.

their effect, one would probably be the direction in which lies the main supply of nutriment, and a firm attachment.

Two opposite possibilities arise from the definition of polarity of the *primitive spindle* thus recognised in Archegoniate embryos. The apical pole may be directed towards the neck of the archegonium, or towards its base. The first may be styled *exoscopic*, the second *endoscopic* polarity (Fig. 405).

The antithesis between exoscopic and endoscopic polarity, with certain exceptions, follows the major lines of affinity in the Vegetable Kingdom. The embryos which are exoscopic include those of all the Bryophyta, together with *Equisetum*, *Tmesipteris*, and *Isoetes*. Those which are endoscopic are found in the Lycopods, certain of the most primitive Filicales, and all Seed-Plants. An intermediate position is taken by certain Ferns, including all the Leptosporangiates. It will be a subject for later consideration whether, and under what circumstances, a transition may be carried out from one type to the other. In either of them the probable consequence will be that *the embryo will assume at first a more or less spindle-like form*, though this may be variously modified and disguised, as will be seen later.

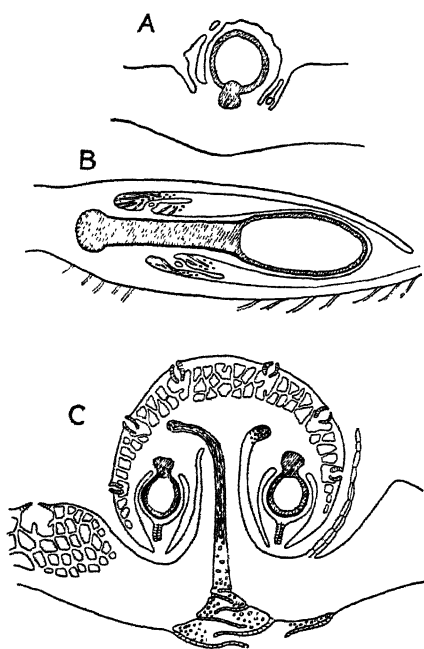


FIG. 406.

Embryos: A, of *Corsinia*; B, of *Monoclea*; C, of *Reboulia*; in their natural orientation. (All after Cavers.) They suggest that in the Marchantiales the polarity is not determined by the orientation of the archegonium relative to gravity.

The Bryophyta are the headquarters of the *exoscopic* polarity, which appears in them with constancy. As a rule their archegonia are not sunk in the tissue of the gametophyte, but project, and are normally orientated both in Mosses and Liverworts, with the neck pointing upwards. But in the latter exceptions occur, especially in the Marchantiales. In these the archegonia are always produced on the morphologically upper side of the thallus, and in simple cases they actually point upwards, as in *Corsinia* (Fig. 406, A). But in others the position of the archegonium may be horizontal, as in *Monoclea* (B); while in the Marchantiaceae, owing to the curvature of the female branches, they may even point vertically downwards, as in *Reboulia* (C). Notwithstanding this, the polarity of the embryo in these plants relative to the

archegonium is unaltered. This shows that gravity and light are not here the determining causes. The appearance is as though a rigid conservatism retained the exoscopic polarity; but probably the biological advantage of a basal source of nutrition from the massive gametophyte has contributed to its maintenance, which allows of a ready liberation of the ripe spores by distal dehiscence. If the direction of the polarity of the embryo is not disturbed by the extreme differences of orientation seen in the Marchantiales, it is no matter for surprise that it should be constantly maintained in the rest of the Bryophyta. For in them the nutrition of the sporogonium is derived mainly from the parent gametophyte, and its development is not complicated by any necessity arising from the establishment of the sporophyte as an inde-

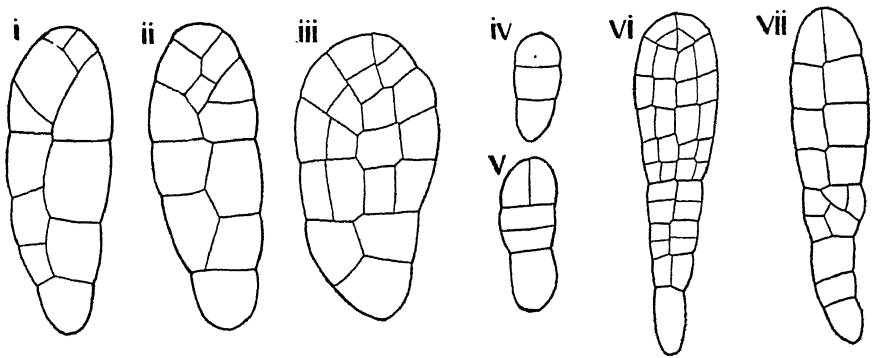


FIG. 407.

Embryos of various Liverworts. i, ii, *Symphyogyna*, same embryo in two aspects (Leitgeb, iii., Taf. v., Fig. 9). iii, *Blasia*, after Leitgeb, Taf. iii., Fig. 12. iv, v, vi, *Radula*, after Leitgeb, Taf. ii. vii, *Scapania nemorosa*, after Leitgeb.

pendent self-nourishing unit. The problem of the exoscopic embryology of the Bryophyta is thus relatively simple.

In the Liverworts the first cleavage of the zygote is transverse, or slightly oblique, to the axis of the archegonium. It is followed in most cases by others in planes approximately parallel to it, so that the embryo takes a spindle-like form, and may appear as though composed of a filamentous row of segments (Fig. 407). But sooner or later, and often very early, the segments subdivide by cleavages in vertical planes. Nevertheless the embryo may still appear as composed of successive tiers of cells, each referable to an original segment (Fig. 407, *iv-vii*, and Fig. 409). In other cases the transverse segmentation may be replaced by alternate cleavages, with a wedge-shaped initial cell. This is seen with less clearness in some Liverworts (Fig. 407, *i, ii, iii*), but it is a marked feature in the sporogonia of the Bryales (Fig. 408).

Lang, discussing the suspensor of Vascular Plants, has drawn attention to the somewhat similar structure at the base of the sporogonium of the

Jungermanniaceae, though it is absent in other Hepaticae.¹ It is sometimes unicellular, but in *Aneura* it may be pluricellular (Fig. 409). Here its suctorial function is obvious from the lobing of the basal cell. Whatever may be the final conclusion as to the strict comparison of such developments with the suspensor of Vascular Plants, the comparison with the similarly constructed organs of attachment of the young plants of many Algae (Fig. 403) seems justified on the ground that they also arise from the base of the germinal filament. The difference is that the latter are free, but the former are enclosed within the maternal tissue.

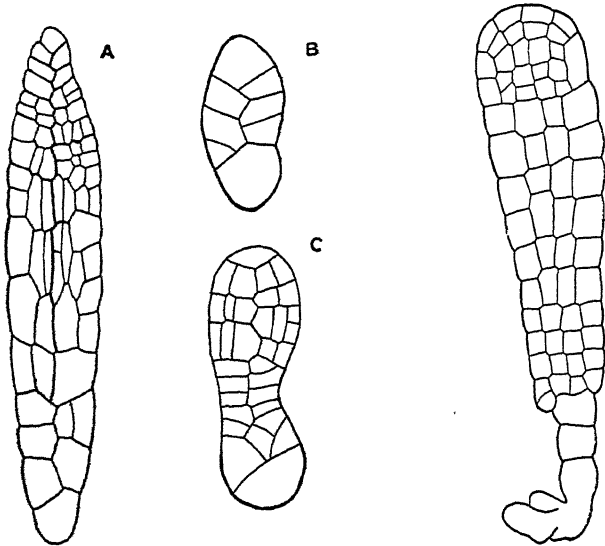


FIG. 408.
Young sporogonia of Mosses. A, *Ceratodon*. (After Kienitz-Gerloff.) B, C, *Nanomirium*. (After Von Goebel.)

FIG. 409.
Embryo of *Aneura multifida*. (After Leitgeb, Taf. ii, Fig. 2.)

There is one exceptional type of sporogonium among the Bryophytes which calls for special notice, viz., that of the Anthocerotales (Fig. 410). Here the embryo seems to differ in its initial segmentation from the rest, and this is in accordance with its adult structure, which shows a highly organised photosynthetic system, and is provided with an elaborate suctorial base. The complexity is due to precocious longitudinal cleavages, so that each flat or segment, *including the basal one*, is divided early into four. The filamentous structure which underlies this more complex state is disguised by those longitudinal cleavages, so that it is not apparent except by comparison. These examples are important as illuminating the state of the embryo in *Imesipteris*, and also that of certain other Vascular Plants where a suspensor cannot be recognised (Figs. 415, 416).

¹ *Ann. of Bot.*, vol. xxviii., p. 35.

All the Bryophytes lack lateral appendages in the sporophyte generation, while Vascular Plants, excepting certain very primitive types, have them. It may then be anticipated that the embryology of the Pteridophyta will be disturbed and less regular in the details of development. Most Vascular Plants also differ from the Bryophytes in the direction of the polarity of their embryos, which is *endoscopic*. These two facts probably account for the slowness of morphologists in realising that a filamentous structure underlies their embryology also. The first general statement on this point was made by Professor Lang (*l.c.*): it followed as a natural consequence from the recognition of the polarity of the embryo of Vascular Plants generally.¹ The form of the Pteridophyte embryo is essentially that of a spindle, the stem-tip being the apex, and the suspensor, when present, the organic base. At first the suspensor was not recognised as a primitive or vestigial part. But Lang regarded the presence of a suspensor in certain Vascular Plants as a last indication of the construction of the plant-body from a filament or row of cells, *i.e.*, of a juvenile stage in the development of the individual rapidly passed over, and often suppressed. In developing this thesis in his Presidential Address at Manchester² he pointed out

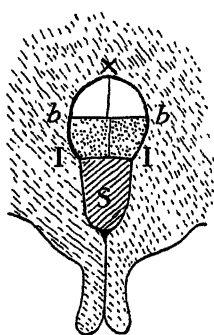


FIG. 411.

Diagrammatic figure of the primary segmentation of the zygote of a Pteridophyte where a suspensor is present, orientated as it would be in the Marattiaceae. S=suspensor. x=apical pole. I, I=first wall. b, b=basal wall.

at last available they may now be examined comparatively from the point of view thus suggested.

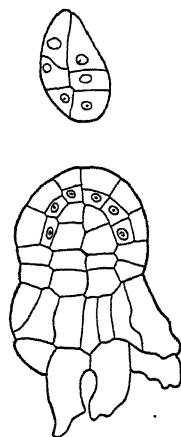


FIG. 410.
Successive stages of the
embryo of *Anthoceros*.
(After Campbell.) $\times 300$.

that his view of the construction of the young sporophyte fits naturally with certain conclusions that may be drawn from the comparative embryology of the Vascular Cryptogams. These are (i) the primary importance of the longitudinal axis of the shoot, the position of the first root and of the foot being variable ; (ii) the constancy of position of the stem-apex near to the centre of the epibasal half of the embryo ; (iii) the probability that embryos without suspensors have been derived from forms with suspensors. He concluded that these and other related facts seem to find their morphological explanation in the shoot of the sporophyte being the result of the elaboration of a filament. Since the essential facts of the embryology of all the leading types of Vascular Plants are

¹ *Land Flora*, chap. xlii., pp. 673-5.

² *British Association Report*, 1915, p. 707.

A general comparison of the embryogeny of the Pteridophytes shows that there are in them two types of primary segmentation of the zygote, according as a suspensor is present or absent. Otherwise there is a remarkable constancy of cleavages. These two types may appear in the same phylum (Lycopodiales, Ophioglossales, Marattiales), and even in the same genera (*Botrychium*, *Angiopteris*); a fact which proves that the difference is not a fundamental one. Where a suspensor is formed the first segment-wall cuts the axis of the archegonium at right angles, and separates the parent-cell of the suspensor from the so-called "embryonic" cell (I, I, Fig. 411). *The suspensor is always directed to the neck of the archegonium, while the embryonic cell, or embryo proper, is turned away from it (endoscopic).* The latter undergoes octant division. As a rule the first cleavage is by a wall parallel to the first, called the basal wall (*b, b*), and it divides the embryo proper into the hypobasal and epibasal tiers: the embryo then consists of a row of three cells. The basal wall is followed quickly in most cases by octant walls, dividing each tier of the embryo into four cells. Meanwhile the form of the whole has elongated in varying degree in different cases, but there is a remarkable uniformity in the initial segmentation wherever a suspensor is present. Where it is absent the whole zygote behaves as an embryonic cell, usually dividing into octants as before (Figs. 417, 418).

An embryo thus constructed may be regarded as a filament or spindle, consisting in the former case of three, in the latter of only two segments, all of which are liable to further subdivision. On comparison with the young of Algae the forms with a suspensor would then represent the more primitive type, as retaining more perfectly the filamentous state. In all of these, whether the embryogeny be free, exoscopic, or endoscopic, the organic apex lies at the centre of the epibasal hemisphere; or as near to it as is consistent with the individual type of segmentation. *The embryo is, in fact, from the first a simple primordial shoot, of spindle-like form.*

RELATION OF THE SPINDLE TO ITS SURROUNDINGS

Regarding then the embryos of Pteridophytes as polarised spindles, however effectively that character may be obscured by the absence of a suspensor, or by the form of the embryo, the next step will be to consider the relation of this fundamentally spindle-shaped body to its surroundings. We have seen that in all Pteridophytes with a suspensor the embryo is endoscopic (Fig. 405), and that the growth of the suspensor has the effect of burying the embryo in the tissue of the prothallus. This is doubtless an immediate advantage in point of nutrition of the embryo in its earliest stage. *But the ultimate end is the establishment of a young plant with an upward-growing shoot suitable for self-nutrition. The orientation of the archegonium will then be a factor affecting the further behaviour of the embryo.* The

most straightforward case is that seen in the Marattiaceae Ferns, where the neck of the archegonium points vertically downwards from the underside of the flat and fleshy prothallus (Fig. 411). Here the embryo will be erect from the first; it breaks through the upper surface of the prothallus and emerges directly as the upward-growing plant (Fig. 412, *i-ii*). A peculiar form is, however, assumed by the embryo of *Macroglossum*, which gives the impression of its being held in place by its suspensor, but unable to penetrate the

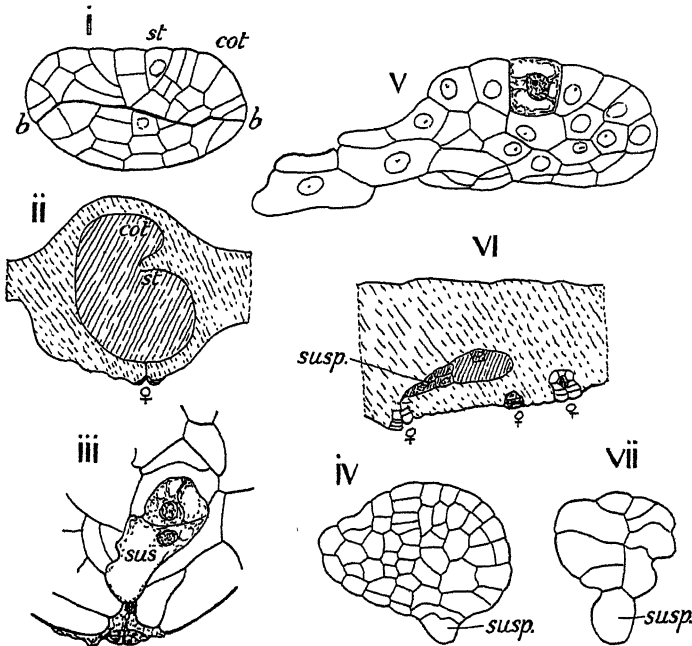


FIG. 412.

Embryos of Marattiaceae. (After Campbell.) *i, ii, Angiopteris*; *iii, iv, Danaea jamaicensis*; *v, vi, vii, Macroglossum*. All are orientated as in nature. *b*, basal wall. *susp*=suspensor. *st*=stem. *cot*=cotyledon. ϕ =archegonial neck.

prothallus upwards (Fig. 412, *v-vii*). Possibly such difficulties as its form implies may have opened the way for the condition constantly seen in the Leptosporangiate Ferns, where the embryo without a suspensor emerges on the lower surface of the prothallus.

It is rarely that the archegonia of Pteridophytes face directly downwards, as they do in the flattened green prothalli of the Marattiaceae. Many prothalli are subterranean. Often they are cylindrical and erect, as in *Ophioglossum* (Fig. 379), and the archegonia projecting from their sides have their axes oblique or even horizontal; but in *Botrychium obliquum* the prothallus widens out into the cake-like form usual for this genus, and the archegonia point obliquely upwards. Here the embryo is provided with a suspensor, and

the embryonic cell is thrust by it deeply into the massive thallus.¹ A curvature will then be necessary in this and in all such cases for establishing the

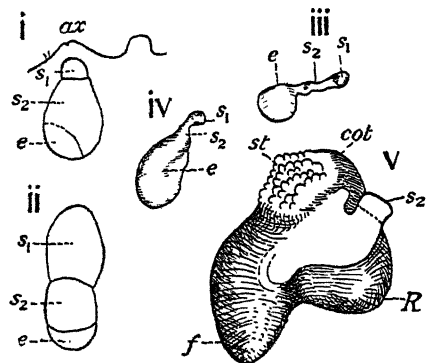


FIG. 413.

Embryogeny of *Helminthostachys*. (After Lang.) i, ii, young arrested embryos, showing orientation to the archegonium (ax). iii, iv, v, reconstructions of three embryos from sections (about 30). s_1 =upper tier of the suspensor. s_2 =lower tier of suspensor. e =embryo proper. st =stem apex, covered with hairs. cot =cotyledon. R =first root. f =foot. iii and v are probably orientated as in life.

upwards, and bearing antheridia and archegonia near to its margin. The archegonia face obliquely upwards; the suspensor points as usual to its neck, and it drives the embryo in the first instance downwards into the thallus. A sharp curvature of its body is then necessary to bring its apical pole to the zenith (Fig. 414).

It can hardly be assumed that such shifts as these should have been attained in the course of opportunist evolution, unless there be some initial disability. It is suggested that the presence of a suspensor, inherited and retained, ties the embryo down to an endoscopic orientation which might be convenient so long as the archegonium points vertically downwards, but is highly inconvenient when it is horizontal, oblique, or upward-directed. The diagrams in Fig. 415, A-E, illustrate this for a number of examples, in all of which the embryo is orientated with the shoot directed finally upwards. The curves which appear in these young

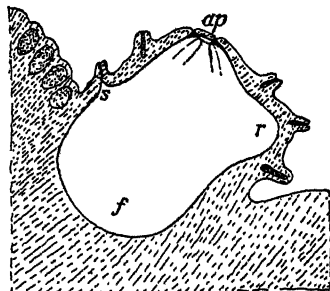


FIG. 414.

Lycopodium clavatum, archegonium and embryo, orientated as in nature, showing curve of the distended spindle, and relation to it of the foot (f) and root (r). (After Bruchmann).

¹ Lyon, *Bot. Gaz.*, Dec. 1905, p. 455; *Land Flora*, p. 471; *Campbell, Ann. of Bot.*, 1921, p. 141.

² See Chapter XXI., pp. 453-4, Figs. 382, 383. ³ Lang, *Ann. of Bot.*, 1902, p. 23.

plants are such as to compensate them for the obliquity of direction of their suspensors; but this was itself dictated in each case by the orientation of the axis of the parent archegonium.

In more than one evolutionary line the simplified form of the embryo may be explained by its having broken loose from the tie of the suspensor. Comparative evidence within the several distinct phyla indicates that an abolition

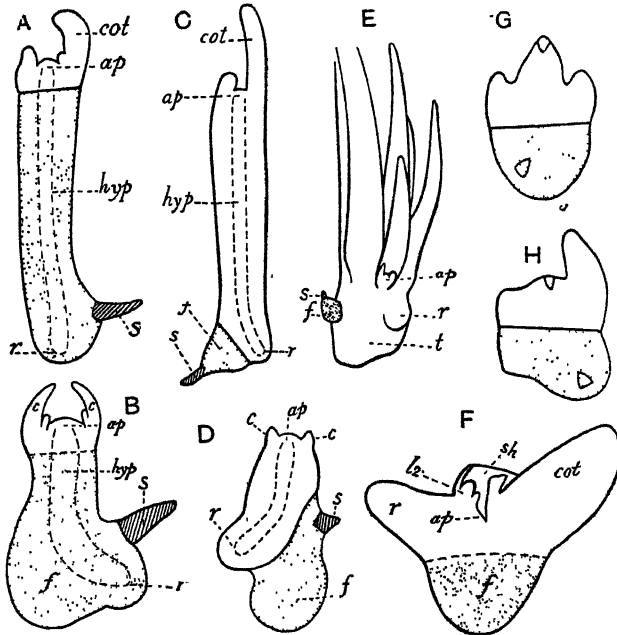


FIG. 415.

Diagrams of embryos. The suspensor is cross-hatched, the hypobasal hemisphere dotted, the epibasal clear. A, *Selaginella spinulosa*. B, *Selaginella Martensii*. C, *Lycopodium Selago*. D, *Lycopodium clavatum*. E, *Lycopodium cernuum*. F, *Isoetes*. G, *Equisetum*. H, *Adiantum* or *Marsilea*. c=cotyledon. ap=apex of axis. r=root. hyp=hypocotyl. f=foot. s=suspensor. These diagrams are all orientated with the shoot pointing upwards; that is, approximately as they would be in nature. A-E show the curvatures by which this is attained: in F, G, H, where there is no suspensor, those curvatures are absent.

of the suspensor has happened repeatedly: for instance, within the families of the Marattiaceae, the Ophioglossaceae, and in the Lycopodiales. The suspensorless state of the embryos of Leptosporangiate Ferns may with high probability be explained in this way. The probability of a progressive loss of the suspensor is supported by comparisons within the single phylum. Among the Marattiaceae *Danaea* and *Macroglossum* have a suspensor, while *Angiopteris*, *Marattia*, and *Christensenia* have none. In the Ophioglossaceae *Helminthostachys* and *Botrychium obliquum* have a suspensor, but *B. lunaria* and *virginianum*, together with the whole genus *Ophioglossum*, have none. In the Lycopodiales a suspensor is regularly present in *Lycopodium* and

Selaginella, but *Isoetes* has none. In all such cases where a suspensor is absent there is also an absence of those awkward curvatures of the sporeling seen in Fig. 415. Hence it may be concluded that these were a disadvantage which has been removed in three separate phyla, and even within the genus *Botrychium*, by the abolition of the tie that caused it: that is, by abortion of the suspensor.

Comparison of the embryo of *Equisetum* with what is seen in the Ophioglossaceae is interesting. Here the archegonia face upwards, or they may be slightly oblique. There is no suspensor, and again the basal wall separating the epibasal and the hypobasal tiers is approximately horizontal, with the epibasal tier uppermost (Fig. 147). It is possible that the history of the

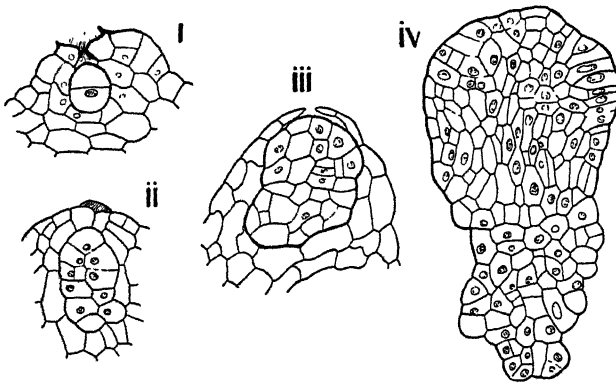


FIG. 416.

Embryos of *Tmesipteris*. (After Holloway.) $\times 100$. They are all orientated with the axis of the archegonium vertical; but in nature it is nearly horizontal, and the polarity of the embryo appears to be also at first horizontal, or inclined obliquely upwards.

origin of this state may have been similar to that in *Botrychium*, involving obliteration of a suspensor. But as the Equisetales are a very isolated group, and the modern *Equisetum* the only one in which the embryology is known, this cannot at present be held as more than a speculative analogy.

The question may be left open whether or not *all* embryos which are without a suspensor are to be accounted for by its abortion. In particular this arises in the case of the suspensorless and leafless embryo of *Tmesipteris*, the prothallus of which may be compared with that of *Ophioglossum* as regards the orientation of the archegonia. Its form is again cylindrical, and usually upright, with archegonia projecting all round it.¹ Their axes are then mostly horizontal, or slightly oblique (Fig. 97). Nevertheless, as Holloway's drawings show, the suspensorless embryo is exoscopic: it consists of two tiers separated by the basal wall, which cuts the axis of the archegonium approximately at right angles (Fig. 416). The hypobasal hemi-

¹ Lawson, *Trans. R.S. Edin.*, vol. li., part iii., p. 22; vol. lii., part i., p. 4. Holloway, *Trans. N.Z. Inst.* vol. i., p. 1; vol. liii., p. 386.

sphere forms a suctorial foot directed inwards : the epibasal faces obliquely outwards, and in its later stages it may curve upwards. Here it appears that gravity, in the first instance, is a less decisive influence on the orientation of the young embryo than the relative position of the prothallial sources of supply : and it is worthy of note that both of the cases where this is so (*Ophioglossum* and *Tmesipteris*) are of markedly mycorrhizic nutrition, which makes early photosynthesis a less pressing necessity than in autotrophic plants. Accordingly, the effect of gravity may well be a less decisive factor for them.

In discussing the spindle-character of the embryo in those cases in which the suspensor is absent the mind should be free from an obsession which the history of the science has left, viz., that the embryo of the Leptosporangiate Ferns or of *Equisetum* should be fundamentally typical for all embryos. The former are relatively late types of the Filicales, and should themselves be interpreted in terms of the Eusporangiate Ferns. *Equisetum* itself, though an old type, is not one of the earliest of the Equisetales. The presumed importance of these embryos has been based on fortuitous circumstances : (i) that the facts of their embryology were among the first to be observed ; (ii) that material for observation is relatively easily obtained ; and (iii) that the segmentations being of a stereotyped plan were relatively easily observed and compared. The argument for their fundamental nature rests on as insecure a basis as that for the priority of the Leptosporangiate Ferns over the Eusporangiate—which is now entirely discredited. An independent attitude should be assumed in this question. In particular, the conception of embryology as a study of cell-mosaics must be abandoned. Wide comparisons not only of embryos but of segmentation at large have shown that while coincidences in the origin of organs in relation to cell-cleavages may exist, they are optional not obligatory for plants at large.

In comparative embryology the megaphyllous Filicales give a more consecutive series of facts than any other class. While *Helminthostachys* (Fig. 413) and *Botrychium obliquum* (Fig. 383) have each a suspensor and a curved, endoscopic embryo, *Botrychium lunaria* and *Ophioglossum* (Fig. 380) have none ; its elimination has made the inversion of the polarity possible, and the embryos of both are exoscopic. Again, while *Danaea* and *Macroglossum* have suspensors, *Christensenia* and *Marattia* have none (Fig. 377). The case of *Angiopteris*, however, is a critical one. All earlier observers have depicted its embryo without a suspensor (Fig. 377, a) ; but Land has demonstrated a well-formed one in specimens from Tutuila (Fig. 378). This may either be interpreted as an organ of immediate adaptive origin, and without morphological significance ; or as a reversion to an ancient feature shared by *Danaea* and *Macroglossum*, but not by *Christensenia* or *Marattia*. The weight of comparative fact, as read in the antiquity of the plants compared, is in favour of the latter alternative. Moreover, no material

change appears to have followed the elimination of the suspensor in the Marattiaceae: the embryo remains endoscopic; in fact, so far as the orientation is concerned, it appears to be immaterial whether or not the suspensor is present in *Angiopteris*. It is in view of these facts and opinions for the ancient Eusporangiate Ferns that the classic example of the Leptosporangiate Ferns may be examined.

The spherical embryo of the Leptosporangiate Ferns is composed of two tiers of cells separated by the basal wall (Fig. 417, *b*, *b*), which is orientated so as to include the axis of the obliquely inclined archegonium. Hence the

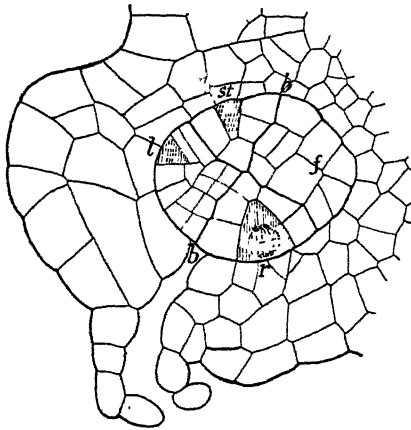


FIG. 417.

Embryo of *Adiantum*. (After Atkinson.) Slightly diagrammatised, and orientated in what is believed to have been approximately the natural position at the time of first segmentation. *b*, *b*=basal wall; *st*=apex of stem; *l*=apex of leaf; *r*=apex of root; *f*=foot.

basal wall is not vertical at its formation, but inclined: and the acroscopic hemisphere is directed obliquely upwards and forwards, while the basiscopic faces downwards and rearwards. The former produces the shoot with axis and leaf, the latter the root and foot. The cotyledon and root both emerge from the lower surface of the prothallus, and this characterises the Leptosporangiate Ferns; but, as already noted, *Macroglossum* may suggest how the transition may have come about (Fig. 377, *vi*). According to our present theory the Leptosporangiate embryo represents only the "embryo proper" of Fig. 411, while the

suspensor has been eliminated. There remains, however, the question of the orientation of the basal wall (*b*, *b*)—slightly oblique to or including the axis of the archegonium—which, though uncommon for other Pteridophytes, is very constant in the Leptosporangiate Ferns. The polarity of the embryo is neither exoscopic nor endoscopic, though there is a bias of the apical pole towards the apex of the thallus. This leads to a relation of all the parts of the sporling which is biologically convenient in providing the earliest possible opportunity for self-nutrition (Fig. 373).

It is difficult to analyse this orientation in terms of the probable factors that determine it. But light is thrown on it by the Hydropterids, the germinating megaspores of which have been experimentally treated by Leitgeb.¹ He found that those of *Marsilia* are large enough to be orientated at will, or grown upon a klinostat. Normally its small prothallus is developed at the apex of the megaspore, with the single archegonium in a median position. As the

¹ Sitz. der k. Akad. der Wiss. Wien, Bd. lxxvii., 1878.

megaspore is oval, it would naturally lie on its side in germination : accordingly the axis of the archegonium would normally be horizontal (Fig. 418). The basal wall will then be horizontal also, since it includes the axis of the archegonium. Leitgeb found that if the germinating spore be submitted to

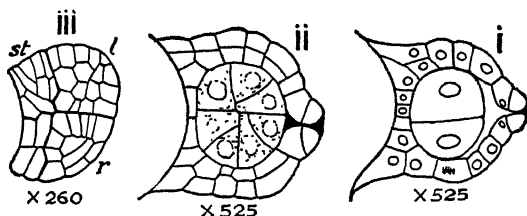


FIG. 418.

Embryos of *Marsilia vestita*. (After Campbell.) Orientated in their probable natural position, since the oval megaspore will normally lie flat on its side, while the prothallus is apical, and the first archegonium median.

various orientation, and even rotated on the klinostat, the position of the first segment-wall in the embryo of *Marsilia* is so far independent of external influences that in every case it includes the axis of the archegonium ; but it is subject to rotation round that axis, and whenever the axis of the archegonium departs from the vertical the basal wall takes a position such that the embryo divides into an upward-directed, epibasal, shoot-forming half, and a downward-directed hypobasal, foot-and-root-forming half. This suggests that a

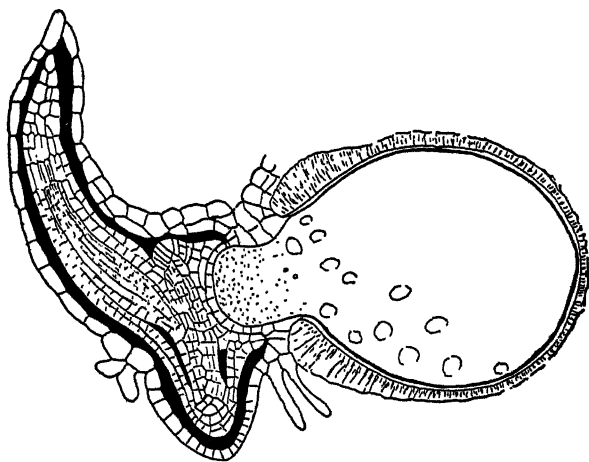


FIG. 419.

Median longitudinal section of young sporophyte and megaspore of *Pilularia*, after Campbell, but orientated as it would be in nature. $\times 70$. The sporangium is still completely enclosed in the enlarged venter of the archegonium.

new tie not represented in other Pteridophytes has been established in the Leptosporangiate Ferns, and markedly in the Marsiliaceae. It has the effect of orientating the embryo at right angles to the axis of the archegonium. Though the actual plane of the basal wall is influenced by gravity, this only applies subject to the condition that the axis of the archegonium is included.

The biological importance of this in heterosporous types is clear enough. As a rule the oval megaspore will germinate on its side. In that case, as the basal wall is horizontal under the influence of gravity, the shoot will always point upwards and the root downwards: as it is seen to be in *Pilularia* (Fig. 419): and this will be secured whatever side of the spore happens to be uppermost.

There remains the embryology of *Selaginella*, which has a special interest, since it is the only living genus of heterosporous Pteridophytes in which a suspensor persists: moreover it is a microphyllous type. The study of it was initiated by Hofmeister, and by Pfeffer,¹ continued into detail for many species by Bruchmann,² and summarised by Goebel.³ Unfortunately illustrative figures have been dominated by a misleading convention: that of considering the embryo in relation to the axis of the archegonium rather

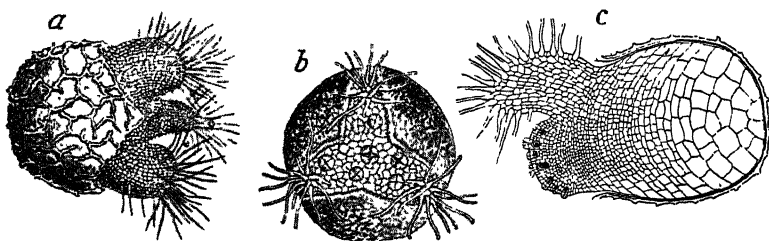


FIG. 420.

Germinating megaspores of *Selaginella*, orientated as they would most probably lie on the soil. (After Bruchmann.) *a*=*S. Galeottii*, showing the three large rhizoid-bearing processes of the gametophyte surrounding the archegonium-bearing area. Microspores are caught among the rhizoids. $\times 205$. *b*=Megaspore of *S. Martensii* presenting its frontal face, with archegonia. $\times 150$. *c*=Median section of megaspore of *S. Galeottii*, with prothallus and archegonia with their axes horizontal. One rhizoid-bearing process is cut in section; the others missed by the median section would have pointed obliquely downwards. $\times 75$.

than in relation to gravity during development. The illustrations of embryos are almost invariably orientated with the archegonia pointing upwards from the more or less oval spore, though in nature the megaspore would more naturally lie on its side, and as a consequence the axes of the archegonia would in most cases be approximately horizontal (Fig. 420). The sporeling commonly shows by the lateral position of the spore at the base of the upward-growing axis that this must have been so (Fig. 421). Doubtless experiment, which still remains to be made on *Selaginella* along lines similar to those of Leitgeb on *Marsilia*, will show the degree and nature of the relation of curvature of the embryo to the direction of gravity. For the present discussion the drawings of germinating spores and embryos borrowed from Bruchmann will be orientated with the apex of the embryo pointing upwards; and it will as a rule be found when that is so that the axis of the archegonium, as

¹ Hanstein's *Abhandl.*, Heft iii., 1871.

² *Unters. u. "Selaginella spinulosa,"* Gotha, 1897; *Flora*, 1908, p. 12; 1912, p. 180; 1913, p. 237.

³ *Organographie*, 1930, Teil ii, p. 1122, etc.

indicated by the suspensor, will usually be directed not upwards, but horizontally or obliquely.

In *Selaginella*, as in other Pteridophytes where a suspensor is present, it is directed towards the neck of the archegonium, and the embryology is endoscopic. The early segmentation of the embryo is essentially as in *Lycopodium* and others (Figs. 219, 411). The epibasal hemisphere is soon flattened, and the apex of the axis originates at its centre, with the two cotyledons, which arise in more or less definite succession, seated laterally. The primitive spindle is defined as lying between the apex of the axis and the tip of the suspensor. This spindle is at first straight; but very soon, as the

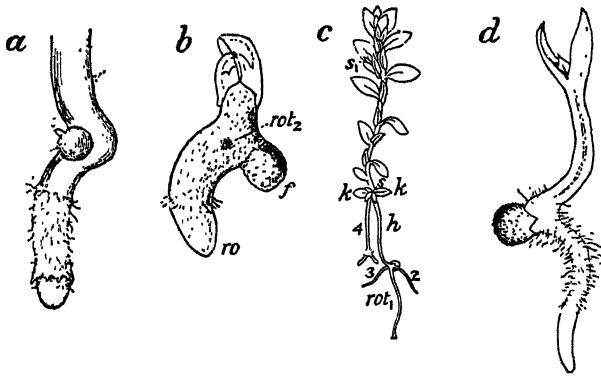


FIG. 421.

Sporelings of *Selaginella* orientated in their probable living positions. *a* = *S. Martensii*, showing upward hypocotyl, and downward first root breaking through the "rhizophore"; to the left the suspensor pointing obliquely upwards, below it the second "rhizophore"; the foot is very slightly developed. $\times 32$. *b* = *S. Galeottii*, relative position of parts the same, but suspensor not seen, and the foot better developed. $\times 45$. *c* = *S. Galeottii*, more advanced plant, with successive rhizophores (1-4). *h* = hypocotyl; *k*, *k* = cotyledons; *s*, *s* = dormant buds. $\times 3$. *d* = *S. Kraussiana*, after Campbell. $\times 12$. *a*, *b*, *c*, after Bruchmann.

hypocotyl lengthens, it is liable to curve, so that the apex takes a vertical position, whatever the orientation of the megaspore may have been. A certain indication of how the axis of the archegonium was orientated in germination in any individual case is given by the position of the suspensor. If, then, the sporelings drawn by various authors be orientated according to their upward-growing shoots, it appears that the orientation of the archegonia from which they sprang has not been uniform. This is the result to be expected as following from the haphazard position of the spores in the soil. But in the majority of cases the oval spore lies naturally on its side; and as the archegonia are borne upon the convex surface of the projecting prothallus their axes will, as a rule, be horizontal or oblique (Fig. 422, *a*, *c*, *d*). Only occasionally will the archegonia point upwards, in which case a complete inversion of the embryo will be necessary. This has almost certainly been so in the megaspore of *S. Kraussiana*, figured by Bruchmann,¹ where the

¹ *l.c.*, 1912, p. 191, Fig. 9.

orientation of the shoot is reversed, the apex finally pointing towards the archegonium (Fig. 422, *b*).

It thus appears that the embryo of *Selaginella* is exposed to conditions not unlike those of *Helminthostachys* and *Lycopodium*, and that it reacts like them by curvature. The primitive spindle is, as in them, tied down by

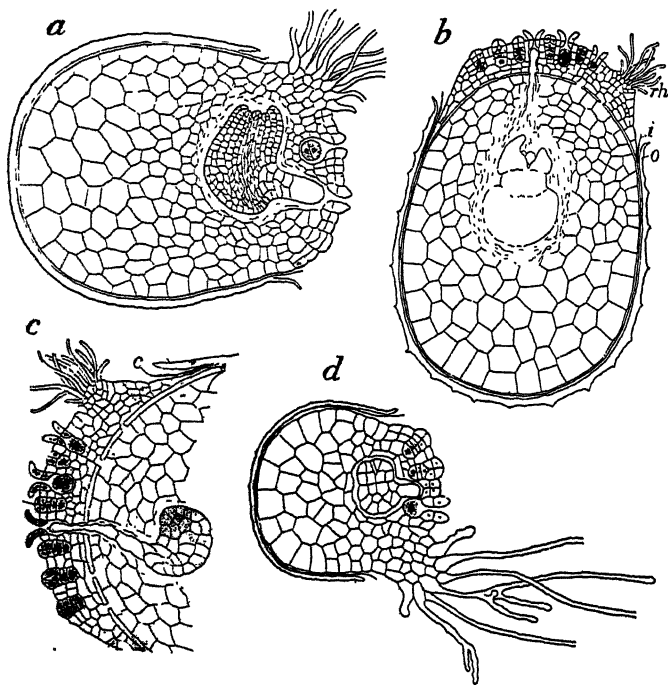


FIG. 422.

Embryos of *Selaginella*, *in situ*, orientated with the axis pointing upwards. (After Bruchmann.) *a*=*S. Martensii*, megaspore and prothallus in median section; the oval megaspore lying on its side, and the apex of the embryo directed upwards. $\times 150$. *b*=*S. Kraussiana*; the embryo with its apex pointing upwards suggests that this megaspore was erect in germination. $\times 112$. *c*=*S. Martensii*, a younger stage than (*a*), showing the same orientation of the spore and embryo. $\times 112$. *d*=*S. rubricaulis*, megaspore and prothallus orientated so that the apex of the embryo points upwards. $\times 135$.

the suspensor to the axis of the archegonium, and it is endoscopic. But the archegonium produced from the detached megaspore may be variously orientated. The facts indicate that the embryo corrects this by curvatures which may be of varying degree. These become intelligible when the drawings of germinated spores are orientated as they probably were in life (Figs. 421, 422). We may conclude from them that the direction of the mass of stored food influences the embryo (either directly, or more probably phyletically) in its first stage of development, so that it buries itself deeply in the prothallus. But as the spindle elongates the response to gravity becomes effective, and leads to those curvatures which are so characteristic of the embryo

of *Selaginella*. Von Goebel remarks that it is unknown whether the curvature is autonomic or induced.¹ When the facts are viewed as above stated there can be little doubt that it is induced, though that opinion still requires to be tested by actual experiment.

The only other living genus of the Ligulate Lycopodiales is *Isoetes*. After fertilisation its megaspore forms an embryo without any suspensor, and exoscopic, though with some fluctuation in the plane of the first cleavage, and apparently some shifting of position of the embryo as it develops (La Motte). The relation of this embryo to that of *Selaginella* may be compared with that of *Ophioglossum* to *Helminthostachys*. In *Selaginella* and *Helminthostachys* contortions of the embryo secure the upward exit of the endoscopic shoot, but in *Isoetes* and *Ophioglossum* the exit of the exoscopic shoot is simple and direct. A further parallel is seen in *Marattia* without a suspensor and *Danaea* where it is present. Thus the embryology in the suspensorless plants would accord with a theory of a primitive spindle, if in each the problem of establishment as a leafy plant be held as having been simplified by the elimination of the suspensor. An alternative view, viz., a sporadic appearance of a suspensor *de novo*, would involve the added complexity of curvature to the problem of individual development, which harmonises ill with evolutionary probability. The special case of *Angiopteris* quoted by Land, where a suspensor is present (Fig. 378), may best be interpreted as a throw-back to the state seen in the related genera of *Danaea* and *Macroglossum*, but eliminated in normal specimens of *Angiopteris*: as it is also in *Marattia*, and in *Christensenia*. This conclusion is, however, one of probability rather than of demonstration.

RELATION OF THE APPENDAGES TO THE SPINDLE

In dealing with any far-reaching morphological question we should distinguish between features that are relatively constant and those which are variable. On the degree of their variability depends the scale of confidence to be placed on those features for purposes of comparison. Reviewing Archegoniate embryos as a whole, *the most constant feature is the polarity of the embryo*: that is, the simple fact that apex and base are distinguishable. This polarity, defined by the first cleavage of the zygote, may be disguised or even partially obliterated in the more advanced types: (i) by the abolition of the suspensor which represents the basal pole; (ii) by an early introduction of longitudinal cleavages which subdivide the single cells of the primitive spindle; and (iii) by amplification of the spindle either by intercalary growth, by its branching, or by the appearance of appendages laterally upon it. Notwithstanding these disturbing features, and allowing for the distortions which follow upon them, *comparison shows that in all fully investi-*

¹ *Organographie*, ii., 1930, p. 1122.

gated cases the apex has a definite relation to the first cleavage of the embryo. It originates—as nearly as is consistent with the embryonic cleavages—*at the centre of the epibasal hemisphere*: that is, in close relation to the intersection of its octant walls.¹ The central point is marked (x) in Fig. 411. *This point and the basal end of the suspensor (where present) define the axis of the spindle.*

The attempt must be made to trace the relation to this original spindle of those constituent parts which, in all but the simplest sporophytes, form the greater part of the adult plant-body. In free-growing Algae, such as *Cedogonium* or *Chaetomorpha*, branching and the formation of appendages may be entirely absent: and similarly in the encapsulated embryos of the Bryophytes the spindle remains simple, excepting a few occasional abnormalities, and certain minor appendages recorded by Von Goebel.² In the simplest Pteridophytes (Psilophytales and Psilotales) dichotomy appears as a marked feature: and this may pass over to monopodial branching, thus producing lateral appendages. Another possible origin is by enation of parts from surfaces previously not tenanted. These matters will be discussed in Chapters XXVII and XXX; meanwhile they are noted as sources leading to the origin of those parts collectively called "leaves." The other parts which appear in early embryology are roots, and those suckorial organs included under the title of "foot." The relation of these several parts to the initial spindle will now be considered from the point of view of their constancy of occurrence and of position.

In the conformation of embryos *the feature next in constancy to the polarity of the spindle is the relation of leaf to axis*, as seen in Vascular Plants. The leaf-formation always arises from the epibasal hemisphere. The leaves themselves appear lateral in relation to the apex of the spindle: their dorsiventrality is more or less marked, and the orientation is such that one flattened side (adaxial) faces the apex. The number and succession of the leaves may vary, but the shoot-nature of the distal end of the spindle, as a whole, in leafy plants is unmistakable. The foliar development followed the definition of polarity in the evolutionary history. Where present, the axis with its constantly related leaf or leaves constitutes the primordial shoot, which represents in a more complex form the originally simple anterior pole of the primitive spindle.

Next in order of constancy in relation to the spindle, but falling in this respect far behind foliar development, is the root. It is absent from all Bryophytes, and from the Psilophytales and Psilotales: also from the floating genus, *Salvinia*. The first root of embryos at large is inconstant in its position relatively to the other parts of the embryo. The genus *Selaginella* illustrates its variability even within a close circle of affinity (Fig. 423). In the embryo of *S. denticulata* (a) the relation of parts is as in *S. Martensii*, the root appearing on the same side of the curved embryo as the suspensor;

¹ *Land Flora*, p. 664.

² *Organographie*, ii., p. 680.

in *S. Poulteri* (b) it is on the side opposed to it; in *S. Galeottii* (c) the root is on the same side as the suspensor, but between it and the apex. Thus in no two of these embryos is the position of the root the same relatively to the other parts. In the Equisetaceae and Marattiaceae there is variety in detail, and some uncertainty as to the origin of the root from the hypobasal or the epibasal region, though the former is constant in Leptosporangiate Ferns. In *Lycopodium* and *Isoetes* its origin is epibasal. In the Leptosporangiate Ferns the first root always arises from the hypobasal hemisphere, on the same side

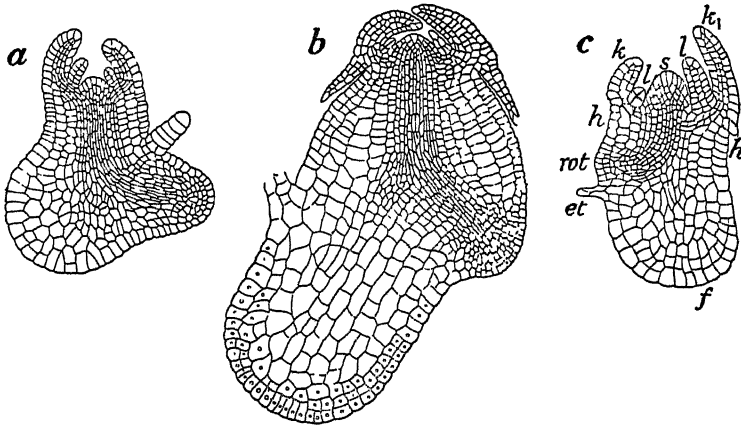


FIG. 423.

Embryos of *Selaginella*, orientated so that their apices shall point upwards, and demonstrating the variability of position of the first root. (After Bruchmann.) *a* = *S. denticulata*, the suspensor pointing obliquely upwards. $\times 150$. Root on same side as suspensor, but remote from apex. *b* = *S. Poulteri*, suspensor pointing obliquely upwards, but root on the side opposed to it. $\times 100$. *c* = *S. Galeottii*, suspensor horizontal, root on same side as suspensor, but between it and the apex. $\times 150$.

of the spindle as the cotyledon; in *Isoetes* it is on the side opposed to it (Fig. 415, F, H). In *Phylloglossum* and *Lycopodium* the first root is exogenous; in *Selaginella* it is endogenous, bursting through the tissue described by Bruchmann as the "rhizophore." In mycorrhizic embryos the root may be hurried forward early, as in *Ophioglossum vulgatum*; in others it may be delayed, as in *Lycopodium* and *Selaginella*. Notwithstanding such variability there is one point in which the root is constant: *in its position relative to the spindle the first root of all Pteridophytes that have a suspensor is clearly lateral*; it projects from the side of the spindle, and is not itself part of it. Where the suspensor is absent it may appear as though the first root formed with the opposed shoot the axis of the whole embryo, as in the Leptosporangiate Ferns. But comparison of early stages of the suspensorless embryos of *Equisetum* or of *Isoetes* shows that the initial position of the first root was lateral in them, though it is more clearly so in those embryos in which the suspensor is present. *The root is thus accessory to the spindle itself, and variable both in position and in the time of its definition.*

If the stigma of instability is applicable to roots, it falls still more heavily on those haustorial organs of the Pteridophyta which have been included under the term "foot." There seems now no reason to revert from the opinion expressed fifty years ago with regard to them.¹ They are so variable in occurrence, in position, in time of development, and in structural characters, that they hardly deserve recognition as a morphological category of parts. *They are, in fact, opportunist growths, formed in positions convenient for the suctorial function.* Their presence tends to disguise, and their absence to reveal the real nature of the spindle.

It thus appears that the root and foot are in a different position from the shoot as constituent parts of the embryo. The shoot represents the distal or apical end of the primitive spindle, the base of which is the suspensor in Vascular Plants, or the seta in the Bryophytes. But the original spindle is liable to be disguised, and its identity obscured partly by the loss of the suspensor, but much more effectively by the accessory growths of the foot and of the root, and by its curvature in response to gravity. It is also obscured by those complicated apical developments which lead to the establishment of the adult leafy shoot. By these a vegetative phase of unlimited plan has been intercalated in Vascular Plants between the base and the propagative region. Spore-production, originally distal, has thus been indefinitely deferred, and even handed on to secondary branchings. But however complete may be the disguise of the primitive spindle, by basal abbreviation, by formation of accessory parts, or by apical elaboration, it is believed that by recognising it as the foundation of the individual sporophyte in all Archegoniate Plants—and ultimately of Seed Plants as well—we bring precision into their morphology. A consistent presentment is thus attained of that simple source from which all their embryos and consequently all their adult shoots are believed to have arisen.²

This treatment of the embryo in the Archegoniatae is essentially organographic. The formal morphology based on cell-mosaics, and developed under the assumption that all embryos must be interpreted in terms of the Leptosporangiate Ferns, or of *Equisetum*, is now superseded. Stark formal comparison, based on cell-cleavages, will not bring natural results. Here the central idea has been to treat the embryo from its first inception as a *shoot-unit*, not as a congeries of constituent members referable to definite categories; but each from the first is held to be a co-operative part of the plant-body. There must also be reasonable consideration of the circumstances under which the individual embryo develops. Moreover, the key positions in comparison must be given to those types which have been shown by wide reference to have been of early origin. Living representatives of palaeozoic types, such as the Psilotales, Lycopodiales, Equisetales, and the Eusporangiate

¹ Bower, *Quart. Journ. Micr. Sci.*, 1882, vol. xxii., p. 277.

² Compare Von Goebel, *Organographie*, 1930, p. 1114.

Ferns, considered biologically, will therefore take a prior place in embryological study. They will help towards the interpretation of the embryo in those of the Archegoniatae which palaeontology and comparison indicate as of later origin: such as the Leptosporangiate Ferns.

Finally, in the light of fossils lately discovered, the Bryophyte sporogonium may be accepted as a general prototype from which to start such embryological comparisons as those included in this Chapter. The simple spindle, upon which the Bryophytes have specialised with such marked success, is in fact the foundation upon which the more elaborate plant-body of the Pteridophytes appears to have been built. The relation of this idea to Zimmermann's theory of the "Telome" will be considered in Chapters XXX and XXXI.

CHAPTER XXVII¹

AXES AND LEAVES

THE title of this Chapter is intended to give a key to the discussion which it contains. If the heading had been "*The Axis and the Leaf*" that would have carried the mind back unconsciously to the old Nature Philosophy. Under its influence all foliar appendages were referred to a single ideal type, as represented by the foliage leaf of the Higher Plants. The preconception that they should be so referred seemed quite natural in pre-evolutionary times, when comparison was habitually based upon the most advanced types, and those of lower organisation referred to these. A plant was then conceived as being built up of parts belonging to certain fundamental categories. Caulome, Phyllome, Rhizome, and Trichome co-operated in the constitution of the vegetative system. There was not even a separate category assigned to include the sporangia; for these were held to be metamorphosed vegetative parts:—the equivalents of axes, leaves, emergences, or hairs, according to their position and mode of origin. This was the rigid nature of formal morphology as reflected in the third edition of Sachs' *Text-book*, a translation of which appeared as an annotated English Edition in 1875. Beneath all this lay the assumption that there was some ideal plan. This was indeed the essence of the Nature Philosophy which filtered into botanical literature: and signs of it persist to the present day whenever we speak of "The Leaf" or "The Stem."

The observational origin of this attitude may probably be traced to the apparent standardisation of leaves and stems in the Higher Plants; to the lateral position of leaves on the axis; to their apparent basal limit from it by the absciss-layer in leaf-fall; and to their prevalent nutritive function, which may, however, be in abeyance when they are diverted by metamorphosis to such uses as protection, storage, and propagation. The definition of the leaf-nature of a part was then based upon the fact that leaves originate laterally below the apex of the axis, that their succession is acropetal, and their source exogenous from the primary meristem; that their tissues are continuous with those of the axis; that they usually grow more rapidly than the stem that bears them, and assume a form different from it. The morphological conception of these two parts was thus correlative: the axis bears

¹ This chapter is based upon an Address given in the University of Leeds, Dec. 1, 1930.

leaves laterally, and the leaf is a lateral appendage upon the axis. The leaf was contemplated as a constant morphological entity: there was as yet no connected theory of its evolutionary origin. But the recognition of the correlative relation of leaf and axis opened the way for Sachs' own later view, laid down in his *Lectures on the Physiology of Plants* (1882), that the Shoot including both is the real unit. This led later to more rational views.

At the back of the old formal morphology lay Goethe's fundamental idea, as first expressed in his *Metamorphosen-Lehre* (1790), and elaborated into a fuller statement in 1817, under the title *Die Metamorphose der Pflanzen*. All the external parts of the shoot were held as referable to metamorphosis of a single organ. By contemplation of the Higher Plants from this point of view there emerged the abstract conception of the Ideal Leaf. Such views were doubtless based upon the earlier expressions of Caspar Friedrich Wolff.¹ He frankly stated that he saw nothing in the plant but leaves and stem, including the root in the stem. For him the stem was originally the prolongation of all the leaf-stalks united together. Thus a purely phytonic theory followed from his study of the Higher Plants. Wolff's system was closely related to the view more elaborately stated later by Gaudichaud.² But the greatest exponent of phytonic theory of more recent years has been Čelakovsky.³ On a basis of demarcation of stem-segments (Stengelgliede) by boundaries which are not clearly defined in Nature, he pieced out the whole shoot so that he was able to deny the existence of the stem itself as an independent member. This may bring satisfaction to minds ready to recognise such boundaries. His whole Memoir has been subjected to severe criticism by Schoute, who in summing up allows that Čelakovsky has shown that it is possible to construct a scheme of thought which fits in with phytonism; but has not brought decisive proof that it is to be taken as truth, since all the facts may be explained otherwise.⁴ While views of the present day are generally out of accord with the older phytonic theories, and particularly with the method of analysis that starts from the more elaborate types of plants, opinions of a phytonic nature are still entertained in certain quarters; but they are now based upon data derived from the comparison of plants lower in the scale.

Various attempts have from time to time been made to bring precision into the boundaries between parts of the adult shoot-unit. They are known as Phytonic, Pericaulome, and leaf-skin theories; while that of the "Phyllorhize" is really a phytonic theory that involves also a root attendant on each leaf. None of these finds a consistent foundation in the embryology of primitive plants, as they should do if the presumed boundaries are of fundamental nature. Students of the morphology which is based upon development as well as upon the adult structure of archegoniate plants will demur to sharp delimitation of the parts composing the shoot. For after all the axis and leaves act together as a physiological whole, and are so initiated

¹ *Teoria generationis*, 1759.

² *Réch. Génér. sur l'Organographie*, Paris, 1841.

³ *Bot. Zeit.*, 1901, p. 79.

⁴ "On Phytonism," *Réc. d. Trav. bot. Néerl.*, vol. xxviii., 1931, p. 82.

in the embryology; also, in evolutionary history, as based on comparison of early fossils, such as the Psilophytales. The shoot-unit of Sachs is the natural, that is the developmental and evolutionary unit.¹

Such preconceptions as underlay the old Nature Philosophy should find no place in evolutionary enquiry, though it may be difficult enough to exclude them in practice. The alternative will be to consider, in relation to the origin and nature of leaves, certain principles under which the organisation of the enlarging plant-body would necessarily progress from simpler to more complex construction; and to follow inductively as far as possible, by observation and comparison in relatively primitive types, the steps of advance in its organisation. Given equal conditions the reaction will probably be in some degree similar in plants of diverse relationship; or, as it is described when of independent origin, "homoplastic."

The conception of *Homoplasy* was due in the first instance to Ray Lankester.² His short paper went far towards clearing up the vague ideas that surrounded the term "Homology" in the minds of early evolutionists. Lankester introduced the idea of "Homogeny," substituting in a more strict sense the word "Homogen" for "Homologue." He defined *Homogeny* as simply the inheritance of a common part, while *Homoplasy* depends upon common action of evoking causes or of a moulding environment upon homogenous parts, or upon parts which for other reasons offer a likeness of material to begin with. The definition was at once adopted by Zoologists. In the Morphology of Plants the reaction was slow. The conception of homoplasy, whether applied to external form or to the internal evolution of tissues, is not even yet recognised as widely as it should be. The present question relates to external form, and in particular to the origin of foliar appendages. Are the leaves of Bryophytes and those of Pteridophytes homoplastic or homogenetic? Are all the so-called leaves of Pteridophytes truly homogenetic? What is the evolutionary relation of either of these to lateral appendages as seen in the Algae? What degree of homogeny really exists in the latter? Comparisons bearing on such matters cannot be held as acceptable when they are based on mere guesses. They would have to be founded on the recognition of compact sequences, within reasonably close circles of affinity, before they could carry full conviction. But this can hardly be expected in the broad question of foliar origin; nevertheless the evidence may suffice to support statements of reasonable probability. In Chapter XXVIII similar questions relating to the internal evolution of tissues will be considered.

At the present time a new aspect of the morphology of the shoot is being rapidly evolved. It is based upon a comparison of plants low in the scale, whether observed in the adult or in the embryonic state; and it has been supported by many recent palaeontological discoveries. There is reason to

¹ On this question, and particularly on the "Phyllorhize" Theory of Chauveaud, see Von Goebel, *Organographie*, iii. Aufl., p. 133; also Bower, *Proc. R.S. Edin.*, vol. xliii., p. 33.

² *Ann. and Mag. of Nat. Hist.*, 1870, vol. vi., p. 34.

believe that though plant-life originated in the water (and a considerable Flora has retained that habit), a new start was made by the vegetation of the land. In accordance with morphological experience elsewhere it may be expected that innovations would arise, not from the more specialised of the aquatic forms but from those that are simple and primitive, such as the Chlorophyceae, and particularly the Isokonts (Chapter XXV). Whatever their source the results of those innovations are represented by the Archegoniatae, with their alternating haploid and diploid phases. Both will have been initiated under like conditions, and, in particular, both are subject to the disabilities of increasing size. In one way or another both must necessarily meet that disability by modification of form, and in land-living plants this is generally associated with the origin of foliar organs. For reasons explained in Chapter XXIV it may be held as probable that foliar development has pursued a separate course in the haploid and the diploid phases of each Archegoniate life-cycle. Consequently the foliar development of either will be homoplastic with that of the other, not homogenetic. Therefore, each should be considered as a separate problem of evolution, though the conditions underlying the origin of both may have been alike, as are also the results. A primary feature of both phases of the life-cycle in Archegoniate Plants is that, as they develop respectively from spore or zygote, they increase in size upwards. The juvenile form is more or less clearly obconical, though in the sporophyte this is apt to be disguised at first by the circumstances of internal embryogeny, and much more in later development wherever there is cambial thickening. The primary increase in size is accompanied by progressive elaboration of form, which has the effect of adjusting the proportion of surface to bulk. This intimate connection between size and form appears even in the moulding of the juvenile stage, and in the initiation of its parts. Such evidence of the incidence of a size-factor should be recognised as one among many that are liable to affect form, even in the earliest stages of the individual.

A. GAMETOPHYTIC LEAVES

A primary obconical development, such as the gametophyte commonly shows on germination, raises difficulties which intensify as the distal growth proceeds. Following the principle of similarity there will be a progressive diminution of the proportion of surface to bulk, which is met in the young gametophyte by change of form. The presentation-surface may be extended inwards by surface-involution, sometimes combined with fission of internal walls, as in the Marchantiales (Fig. 391, c); or there may be various outward mouldings of the external surface, resulting in a foliar development, as in the Jungermanniales, and in the Mosses (Fig. 395: also Figs. 24, 27, 40, 41, 48, etc.). In the Pteridophytes we note the irregular lobes of the prothallus of *Equisetum* (Fig. 146), and of some species of *Lycopodium* (Fig. 200); or

the flattened form of the obcordate thallus in Ferns (Fig. 364). These mouldings are all effective in tending to maintain the proportion of surface to bulk. An interesting feature in all of them, excepting the leaves of Mosses and Jungermanniales, is the absence of standardisation. The irregular lobes of the thalloid types appear as though they were immediate responses to meet a physiological difficulty, rather than as stable units. It may be asked, why has the development of the gametophyte never progressed beyond small size and simple structure? A probable reason is that here the maintenance of the presentation-surface has been secured *either* by an imperfect surface-involution, with or without the formation of intercellular spaces, as in the Marchantiales; *or* by surface-moulding, as in the leafy Liverworts and Mosses. But no living gametophyte has successfully combined the two methods, after the manner habitually seen in the sporophyte (Chapter XXV). The result is that on land the haploid phase has never reached large dimensions, with a really effective foliar development.

These relations of Size and Form are more readily noted in the young gametophyte of the Archegoniatae, with its free germination from the spore, than in the sporophyte where the embryo is encapsulated. In the former they have a special value in suggesting, as separate causal adjustments, on the one hand the origin of internal ventilation, and on the other foliar development. Whatever view may be held as to the causal relation, there is no room for doubt of the fact that presentation-surface does tend to be maintained by either method, but that foliar development is specially important where, as in the gametophyte, internal ventilation is habitually absent.

B. SPOROPHYTIC LEAVES

Introductory

The sporophyte of the Archegoniatae combined elaboration of form with internal ventilation at an early stage of its evolution. This accords with the relatively simple form and bulky texture of the diploid phase, and of its parts. But ventilation appears to have preceded the origin of appendages, for it is seen in the Anthocerotales and in the Rhyniaceæ.

Those parts of the sporophyte which have been collectively styled "leaves" have been generally distinguished on the one hand as "*megaphylls*," usually of large size; and on the other the relatively small "*microphylls*."¹ The validity and the evolutionary meaning of this distinction presents a problem which can only be solved by comparison between various types living and fossil, aided where possible by reference to individual development. But the facts of embryology, however essential, cannot be

¹ This distinction was primarily due to Prof. Lignier, of Caen, in a series of *Memoirs*, of which the most important are "*Equisétales et Sphénophyllales*," Caen, 1903, and "*Sur l'Evolution Morphologique du Règne Végétal*," 1908-9. Assoc. Franc. pour l'Avanc. d. Sciences.

directly relied upon here, partly owing to the absence of such data in the fossils, partly to the circumscribing influence of internal embryology. The early appearance of the appendages in the ontogeny also tends at times to obscure their relation to the axis that bears them, though still the polarity of the embryo as a whole is defined from the first, and this frequently stamps the relation of the appendages to the axis. Anatomical detail also casts useful sidelights upon the question. But the best way of approach to an understanding of the evolutionary relations of the appendages to the axis, and of the two types of leaf to one another, will be through comparison of leafy plants in the adult state with those primitive sporophytes in which they are either absent or long delayed in the individual life. For this the Bryophytes generally, the Psilophytales, and the Psilotales provide the most suggestive material. These will then lead on to others, such as the Lycopodiales, Articulatae, and Filicales, in which the foliar nature is more definite, whether as megaphylls or as microphylls.

The various sporophytes now known present a sequence of formal steps between two extremes, and it may be traced comparatively without attempting to recognise the examples as phyletically related. On the one hand would be the dependent spindle, without roots or any branching: it is characteristic of the Bryophytes; on the other an independently rooted and leafy plant characteristic of the more elaborated Pteridophyta, and of leafy plants at large. Between these extremes the Psilophytales take a natural place, and their leafless and rootless state shows that in Vascular Plants a photosynthetic shoot existed as a morphological unit before the segregation of its parts. Thus the recognition by Sachs of the unit-character of the shoot now finds its full justification in observed fact.

In the Bryophyta the sporogonium has made the best of the simple dependent spindle, with its distal capsule. The details have been discussed in Chapter VI: in particular steps have been traced in the localisation, and in many instances the final loss of its photosynthetic function. The type in which the segregation of the photosynthetic and propagative regions is least marked is that of the Anthocerotales, and on that account they were accorded by Von Goebel a primitive position in the Class. Attention was thus focussed on them (Figs. 3, 7, 9). But as an efficient plant their sporophyte suffers from the absence of apical growth and branching; and from the want of a definitely organised conducting tract: further, though physiological independence seems to have been approached in *A. fusiformis*, full freedom was never attained. The supply of these deficiencies would be the chief change required to place the type of the Anthocerotales on an equal footing with fully equipped Vascular Plants. On the other hand, the simpler Psilophytales possess certain of those features in which the sporogonium of *Anthoceros* is defective (Fig. 79). Apart from the one being physiologically dependent and the other independent the most important differences are that

Hornea and *Rhynia* possessed apical growth, and an organised conducting system : while they also show repeated dichotomy. In both, as in *Anthoceros*, a superficial photosynthetic system is present, and the distal capsules are not strongly differentiated from the vegetative tract (Figs. 80, 83). Certain branches, however, in *Hornea* and *Rhynia*, similar to those that are fertile, bear no sporangia : this is a primitive form of sterilisation. Such comparisons do not connote real relationship between any living Bryophyte and any known Vascular Plant. They indicate rather a parallel adjustment to similar conditions of sub-aerial life in two types of relatively primitive land-plants, of which one is more advanced than the other ; *but neither type bears organs that can rightly be designated leaves, though in the Rhyniaceae dichotomy is a marked feature.*

C. CLADODE LEAVES, OR MEGAPHYLLS

A dichopodial development of the primary forking of the sporophyte is presented by the Psilophytales. It is shown in the reconstructions of the Rhynie Plants by Kidston and Lang (Figs. 78, 79), and these are supported by the restorations of Kräusel and Weyland, based on the fossil slabs from Elberfeldt (see Frontispiece).¹ The result is the first step towards the differentiation of an axis and cladode leaf. The method of progression, from equal distal dichotomy by gradual steps of inequality to a central rachis with lateral appendages, was first worked out by Prantl, in his *Memoirs on the Hymenophyllaceae and Schizaeaceae*.² But here it was observed in leaves only, with apparently lateral pinnae as the final result. In 1884 the enquiry was extended to the leaves of the Marattiaceae, and other Ferns,³ and the suggestion was made that a similar dichopodial progression may account for the relation of lateral leaves to the axis that bears them, the result being a leafy shoot. Potonié also upheld a similar view : but it was based upon comparisons with Algae, in which dichopodial branching is frequent.⁴ It is a common method by means of which many primitive organisms with a fixed base secure an added range of exposure : in fact it is a convenient way of forming a long stalk. Incidentally the weaker limbs of the original forking become more and more side-tracked, assuming a definitely lateral position ; finally, those formed earliest may originate not distally but laterally below the apex of the axis that bears them. There is thus a gradual transition from distal dichotomy to monopodial branching. Fern leaves illustrate fully the steps from one type to the other (Fig. 238).⁵ The question raised in 1884, whether this would also account for the origin of the relation of leaf to axis in a mono-

¹ *Abh. Senck. Naturforsch. Ges.*, Bd. 40, Taf. 14.

² Leipzig, 1875, 1881.

³ Bower, *Phil. Trans.*, 1884, part ii., p. 605.

⁴ *Naturwiss. Wochenschrift*, 21, Berlin, 1899.

⁵ See also Bower, "Leaf Architecture," *Trans. R.S. Edin.*, 1916, ii., p. 657.

podial shoot, was left for the time open, owing to deficiency of demonstration by facts in any known vascular plant. The discovery of the Rhynie plants with no sharply marked axis and leaf, but only dichopodial forking, gave examples of that early state of branching which was required to make the suggestion of 1884 valid. For in the Rhynie plants distal dichotomy is present, with dichopodial development, which may be held as suggesting the distinct cladode leaf and axis in the making from an indeterminate forking of a simple shoot.¹ A like branching has been demonstrated for the "leaf" of *Stauropteris* by P. Bertrand (Fig. 424). Here, whether or not the so-called

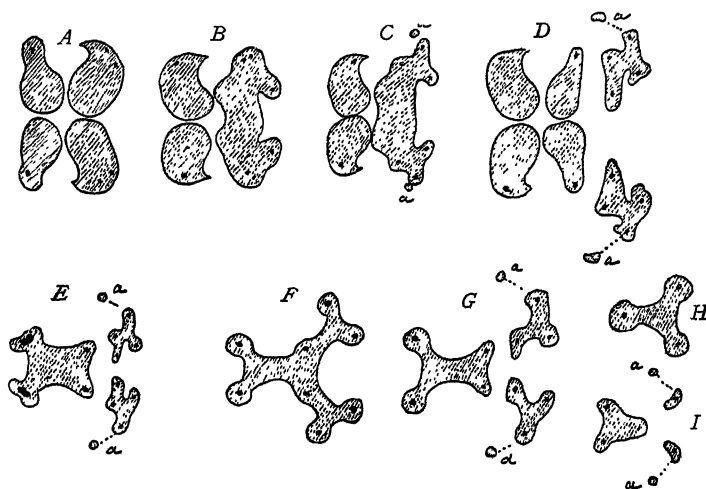


FIG. 424.

Vascular supply to the ramifications of *Stauropteris*, after P. Bertrand. The protoxylem is represented by black dots. *A*, a rachis of the first order, showing a mean condition of the four ylem-tracts; *B, C, D*, stages in the departure, on the right, of the supply to two pinnae of the first order; *a*, aphlebia-traces; *E*, rachis of the second order, showing undivided xylem, from which pinna-traces of the second order have been detached, with their aphlebiae (*a*). *F, G*, stages in the departure of triangular traces for pinnae from the triangular xylem-tract of a rachis of the third order; *H*, triangular trace of the fourth order; *I*, the same, giving off traces to pinnules and aphlebiae (*a*). Compare Fig. 1 with Figs. *D, E, G*, which together illustrate the progressive simplification of the smaller branchlets. It is on the ends of these that the sporangia are borne.

leaf is actually a substantive shoot, it is seen that the dichotomies are not restricted to one plane, a condition that was probably general for early fern-like plants; but the cladode soon settled down to branching in a single plane.²

If the preceding sketch gives a true picture of the genetic relations of axis and megaphyll the anatomical structure of both should be alike, at least in the earliest types. This argument was advanced by Tansley in 1908, with positive results.³ The structural resemblance of axis and petiole has since

¹ Kidston and Lang, *Trans. R.S. Edin.*, lii., pp. 838-845. Here a full discussion of the bearing of the Rhynie Plants on the origin of the organisation of the shoot in Land Plants is given.

² P. Bertrand, *Progressus Rei. Bot.*, vol. iv., 1912.

³ *New Phytol.*, Reprint, No. 2.

been confirmed in *Botryopteris*¹ and in other early Ferns (Fig. 431). In relation to this the facts recorded for the Devonian fossil, *Aneurophyton*, by Kräusel and Weyland, have a special value. They found that the large leaf-like blades of this plant possess the same characteristic structure as the parts which they recognise as the axis.² Thus external form and internal structure support the view that, however highly elaborated or modified, *the axis and cladode leaf as seen in Ferns are referable in origin to a common scheme of distal forking*. The further architecture of the blade in the Filicales, with its webbing and venation, has been sufficiently dealt with elsewhere.³

D. MICROPHYLLS, OR THURSOPHYTON-LEAVES

Such dichotomy as that above described is illustrated in *Asteroxylon* not only by the main trunks but also by those small "*Hostimella*" twigs which bear sporangia. The facts added by Kräusel and Weyland from their Elberfeld material may be accepted as proving for that species the connection of these with the main trunk, a point which had been left open by Kidston and Lang for *A. Mackiei*. But in addition to the subordinated branch-systems recognised as of cladode nature, *Asteroxylon* bears also small and simple "leaves" laterally upon the main dichotomising shoots, which suggest an

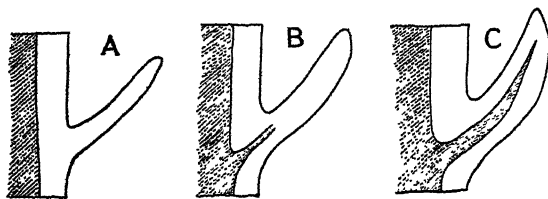


FIG. 425.

Diagrams of spines (microphylls or Thursophyton-leaves) of Psilophytales, showing their relation to the stele of the axis. *A*, as in *Psilophyton princeps*, where there is no vascular supply to the individual spine. *B*, as in *Asteroxylon*, where a strand approaches the base of each, but stops short without entering it. *C*, as in *Arthrostigma*, where a vascular strand enters the base, and extends towards its tip. These figures are based upon observations by Lang, but have not been constructed according to scale. The vascular tracts are shaded.

origin different from theirs (Fig. 79). Here as in the living Psilotaceae the rhizome though branched is leafless; but there is a gradual transition upwards from this to the leafy shoot. Passing upwards again in *Asteroxylon* these small leaves fade out, and the distal "*Hostimella*"-twigs are again leafless. The plant thus consists of three regions, of which the middle region only, which is the most robust, bears these small and crowded leaves (Frontis-

¹ Miss Bancroft, *Ann. of Bot.*, xxix., p. 531.

² *Beitr. z. Kennn. d. Devonflora*, iii., 1929, p. 320.

³ See Chapter XVI; also Bower, *Ferns*, vol. i., chap. v., and Von Goebel, *Gesetz-mässigkeiten im Blattaufbau*, Jena, 1922.

piece). They resemble the microphylls of the fossil *Thursophyton*. Two different types of foliar appendage are thus indicated: the cladodes or megaphylls, which originate by distal dichotomy; and the microphylls, or "*Thursophyton*"-leaves, to which no such origin can be ascribed. But in this *Asteroxylon* does not stand alone. Appendages of a similar nature to its microphylls, though rather more spinous, are found in *Psilophyton* and *Arthrostroma*, of Lower Devonian age. Their presence upon the larger stems, and their infrequency or absence on the slender axes, corresponds to their distribution in *Asteroxylon*. Their structure is also in general accord. The smallest microphylls of *Asteroxylon* are found on the transition region from the rhizome, and they are simple cones of parenchyma without vascular supply:¹ in those that are larger there is an epidermis with stomata, while leaf-traces approach the bases of the leaves, but do not enter them.² In the spines of *Arthrostroma*, however, a strand of tracheids traverses the centre of the appendage, and there is an epidermis with well-formed stomata. On the other hand, in *Psilophyton princeps* there is a vascular strand in the main axis, but no vascular supply to the spines themselves, nor even approaching their base. In many cases these spines have been shown to have a peculiar apparently glandular tip. Another interesting feature is seen in this plant, viz., that large and small spines may occur close together on the same stem surface. These facts relating to very early fossils may be compared by the aid of



FIG. 426.

Psilophyton Goldschmidtii, somewhat reduced from natural size. From Halle, *Plants from Roragen*, 1916, p. 22.

diagrams constructed on the basis of photographs by Dr. Lang: they appear to illustrate progressive steps in complexity of structure in microphylls. It need not be assumed that they possess phyletic significance, though they are taken from plants recognised as akin, and of early Devonian time (Fig. 425, A, B, C). Thus from the fossil evidence we are led to contemplate microphylls as of progressive development, and distinct in origin and in history from megaphylls. Both may be present on the same individual plant; a classical example of this is seen in *Psilophyton Goldschmidtii*, quoted by Halle from Nathorst (Fig. 426): here are borne upon a relatively main axis smooth subordinated lateral twigs of cladode type, and also microphyllous spines; but the latter are absent from *Hornea* and *Rhynia*: also from *Zostero-*

¹ K. and L., iii., Pl. iii., Fig. 23.

² *l.c.*, Pl. iv., Figs. 37, 38.

phyllum. Such facts suggest that they are parts superadded upon a fundamental branch-system.¹

The two living genera of the Psilotaceae also bear in their vegetative region appendages comparable in position and origin to these "*Thurso-phyton*"-leaves or microphylls (Chapter VIII, Fig. 90 *bis*). As in *Asteroxylon* the lower part of these plants bears none of them; moreover, the embryo of *Tmesipteris* gives no sign of early foliar organs (Fig. 416). They appear in the living genera only as the stem advances upwards. In *Psilotum*

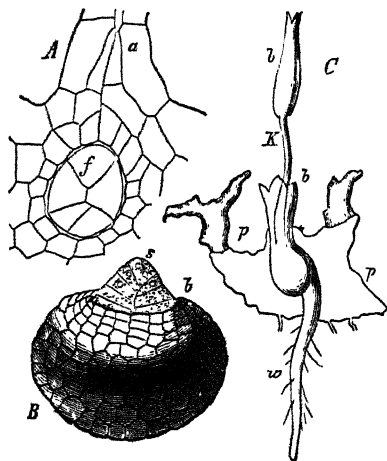


FIG. 427.

Development of the embryo of *Equisetum arvense*, according to Hofmeister. *A* = archegonium cut through vertically with the embryo. *B* = older embryo isolated; *b* = annular leaf-cushion; *s* = apex of the first shoot. *C* = vertical section of a lobe of the prothallus (*p, p*) with a young plant (*K*); *w* = the first root; *b, b* = the leaf-sheaths. *A* and *B* > 200. *C* > 20.

the sparsely scattered microphylls are always small, consisting, like the smallest spines of *Asteroxylon*, of an epidermis and mesophyll, but without stomata or vascular supply: though a strand may sometimes be traced from the stele to their base (compare Figs. 91 *bis, a*, and 425, *B*). In *Tmesipteris* the earliest microphylls are equally simple; here, however, the adult "leaf" is a laterally compressed, relatively large body, with numerous stomata and a vascular strand (Fig. 90 *bis, c*). But it bears as a distal "mucro" a body corresponding structurally to the original microphyll. This more complex appendage has been referred in Chapter VIII to the intercalation of a basal region of indeterminate character between the axis and the microphyll.

These facts, and particularly those of the embryogeny, accord with an *upgrade reading of the origin of the microphylls of the Psilotaceae as enation-leaves: that is, as new formations from a surface previously untenanted.*

Comparison within the Psilophytales and Psilotales is thus seen to suggest a progression from microphylls of very simple structure towards those having a more full equipment of photosynthetic tissue, stomata, and vascular supply. It also points to an initial localisation of microphylls on parts that are relatively robust, and exposed to the air, the rhizomatous region below and the distal fertile twigs being free from them. But such restriction does not hold for other microphyllous Pteridophytes: in most of them the distribution is wider. Even in the Psilotales, though the basal region and the embryo itself bears none, in the distal fertile region microphylls are associated with the

¹ For further details see W. H. Lang, *Phil. Trans.*, B., vol. 219, pp. 133, 421, 1930-31; also *Trans. R.S. Edin.*, vol. lvii., 1932, p. 491.

synangia. On the other hand, in the Equisetales and Lycopodiales the embryo is from an early stage supplied with foliar organs, which graduate into the normal microphylls (Fig. 427; compare also Figs. 208, 211, 219). In their distal fertile regions microphyllous bracts are usually, though not always, associated with the sporangia and sporangiophores. Broad facts such as these raise the general question how far the very primitive microphyllous plants, with their limited distribution of microphylls, are to be regarded as illuminating the morphology of the shoot in vascular plants at large, and particularly in those where microphylls are distributed through the whole length of the plant.

A very general habit has been to look upon microphylls as reduced. This is a legacy left to morphology by the old practice of interpreting all plants according to the experience gained from study of the more elaborate types. It involves an essentially pre-evolutionary outlook. It results in a downgrade interpretation of features presented by the most primitive plants of the land. But the reverse should be the initial attitude. An upgrade reading of the morphological data of these earliest land-plants should be assumed, until some sufficient reason is adduced in any specific case, for holding reduction as probable. Applying this principle to the case of the Psilophytales and Psilotales, their ontogeny would illustrate a progression from leaflessness to the presence of *enations* of small size and simple structure, such as the spines of *Psilophyton* or the first microphylls of *Psilotum*; and onwards to efficient photosynthetic organs with stomata and a vascular strand, as in *Arthrostigma* or *Tmesipteris*. There is no reason to demur to such a progressive morphological elaboration accompanied by utility. The addition of enation-leaves would certainly increase the photosynthetic capacity. Such ancient and leafless types as *Hornea* and *Zosterophyllum* would by comparison naturally take their place as primitive. The alternative to this would be that they are simple by reduction to the point of "ablast" (Eichler). The morphology of the future must avoid such a *reductio ad absurdum* as this by attuning itself with due limitations to upgrade views. The correctness of this progressive outlook is thus attested primarily by the negative features seen in the earliest vascular plants of the land; but it also finds support in the morphology of the distal strobilus: particularly in those of the Lycopods, Sphenophylls, and Horsetails. (See Chapter XXIX.)

E. THE LEAVES OF EMBRYOS

The recognition of two types of foliar organs respectively as *megaphyllous cladodes* and *microphyllous enations* will necessarily raise critical problems in respect of the embryonic leaves, and their relation to those of the adult. In *Tmesipteris*, the only member of the Psilotales or Psilophytales in which the embryology is known, the embryo bears no leaves at all (Fig. 100). In

Equisetum, the only type of the Articulatae in which the embryology is known, the embryo is clearly a simple shoot with its first verticil of leaves similar to those of the adult shoot, surrounding the apical cone which is defined before they appear. There is no doubt here of the lateral origin of that verticil, or of the microphyllous nature of the leaf-teeth that compose it (Fig. 427). Turning to the Lycopods, in *Selaginella* the cotyledons with their ligules arise laterally beside the already-defined distal apex, and are clearly of the same nature as the later microphylls (Figs. 218, 219), and the conclusion will be the same as in *Equisetum*. But the plastic embryogeny of *Lycopodium* is not so easily interpreted. The first leaves of *L. Selago* fall readily into line with normal microphyll-development (Fig. 208); but the type of *L. cernuum* seems to diverge (Fig. 213), and particularly the strange developments seen in *L. laterale* (Fig. 428). If, however, it be admitted that the normal microphylls are by hypothesis enations, and often irregular



Fig 428.

L. laterale. 66, young plant with fully developed protocorm and young stem-axis. $\times 4$. 67, young plant with branched protocorm and two stem-axes $\times 4$. 68, 69, do. with young stem-axis and first root. 68 $\times 4$. 69 $\times 5$. (After Holloway.)

in their disposition on the normal Lycopod shoot, while in these tuberous embryos the early development is disturbed by mycorrhizic symbiosis and storage, the most natural interpretation of them will be to see in them modifications of the normal microphylls of the *Selago*-type. Thus each embryo may be read in terms of a microphyllous shoot, but with the enation-leaves more or less irregularly disposed and developed early. They would, as compared with what is seen in *Asteroxylon* or *Tmesipteris*, have penetrated precociously backwards to the earliest stages of the axis; but finally all their irregularities merge upwards into leaves of the normal microphyllous type. The variants are interesting, but it is doubtful whether far-reaching deductions can rightly be based upon them.¹

With such conclusions as these drawn from microphyllous embryos what is to be the interpretation of the embryo in megaphyllous Ferns? This ques-

¹ The older morphologists used the word "Prolepsis" as connoting an anticipatory development; events or developments thus advanced were styled "proleptic": those words being borrowed from grammarians and rhetoricians. There is no need to perpetuate these terms; they are mentioned here to show that the conception is not a new one. For us "anticipatory" and "deferred" will sufficiently convey the ideas on the one hand of basipetal spread of enations to an earlier phase of the ontogeny, where such parts were not originally present; or on the other of their invasion of a distal region, such as the strobilus originally devoted to propagation without their aid.

tion was left over from Chapter XXVI, since its solution turns upon the distinction between megaphylls and microphylls. Is the first leaf of a Fern-sporophyte the equivalent of the first leaf or leaves of a microphyllous Lycopod or of a Horsetail; or is it of cladode nature? In such questions preference should be given to comparisons drawn from the adult shoot rather than to details of an encapsulated embryo, for these are subject to plastic differences even within the limits of a single genus. It has been seen that the adult leaves of Ferns are of cladode nature. Is the first leaf of the embryo also open to this interpretation? A guide towards a decision will be by reference to the most

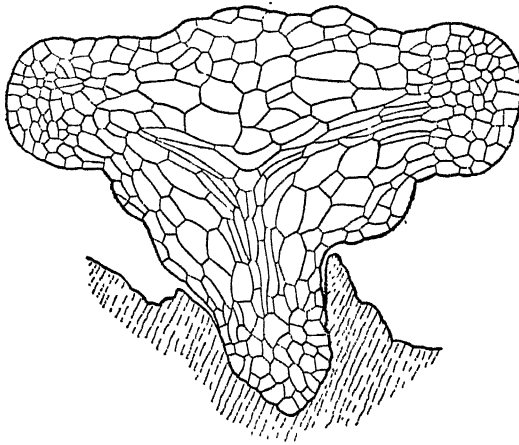


FIG. 429.

Young sporophyte of *Tmesipteris* still attached to the prothallus, cut in longitudinal section, and showing two equally developed shoot-regions. (After Holloway.)

primitive embryology that is known in vascular plants, viz., that of *Tmesipteris*. Holloway has shown that the embryo is at first without any leaf, but that indications of forking of the shoot may sometimes be seen in relatively early stages (Fig. 100, iv): in a more advanced state the equality of such dichotomy is shown by the diverging vascular tracts (Fig. 429). If a forking were initiated still earlier in the individual, and the shanks unequally developed, their relation would be comparable to that of the axis and first leaf in the embryo of a Leptosporangiate Fern (Fig. 417). The inference is that the developmental data are compatible with the view that the first leaf of a Fern is also a result of very early dichotomy, and of cladode nature: a view supported by its own dichopodial tendency in primitive types of Ferns (Figs. 238, 241). From a biological point of view this forking that gives rise to cotyledon and axis initiates at the earliest moment the necessary photosynthetic organ, and by its means the prompt establishment of a self-nourishing plant. This conclusion is not advanced as a demonstration, but as a reasonable organographical probability, based on comparison with the facts observed in

Tmesipteris on the one hand, and upon the adult shoot of Ferns on the other. In point of evolutionary history the first leaf of a megaphyllous plant would then be a cladode-leaf, resulting from distal dichotomy advanced to an early phase of the embryogeny; the first leaves of a microphyllous plant would be enation-leaves, of lateral origin, but formed by anticipation in earlier stages of the individual than in such primitive types as *Tmesipteris* or *Asteroxylon*.

It is probable that this conclusion will not prove generally acceptable: particularly to those who have grown up under the "mosaic" study of embryology, combined with the old assumption that all leaves are in some vague way homologous. Already the limits of legitimate comparison according to segmentation have been unduly strained. It has been repeatedly shown that correspondence between organogeny and segmentation though permissive is not obligatory.¹ Such comparison proves to be a less secure guide than that founded on the adult state as seen in the plants compared. This has led in the present case to the conclusion that megaphylls have originated by distal dichopodial forking, but microphylls by enation from surfaces previously untenanted. The similarity of appearance presented by these parts in the embryo is probably related in both cases to the need for early development of the photosynthetic equipment, combined with the limiting circumstances of encapsulation. Those conditions may well have moulded these parts, of essentially different history but of like function, to such structural uniformity as to disguise their historical difference.

F. DERMAL APPENDAGES IN FERNS

If the first cotyledonary leaf of a Fern sporophyte be accepted as a cladode leaf, and consequently the whole shoot as of dichopodial origin, the question arises whether in Ferns so constructed there are any parts comparable with those enations which appear as "spines" in some of the Psilophytales, or as definitely photosynthetic "leaves" in various Microphyllous Pteridophytes? Lang's recent observations on early Devonian fossils have shown that various degrees of development of those spinous appendages existed, differing in degree of photosynthetic equipment, and in vascular supply (Fig. 425). Thus in these plants spines and photosynthetic microphylls appear to have been forms of the same type of appendage. The relation of these appendages borne upon the shoots of the Psilophytales, and also of the Psilotales, and of microphylls generally, to the parts that bear them is comparable in point

¹ *Land Flora*, chap. xiv. See also D'Arcy Thompson, *Growth and Form*, p. 200. He there quotes Whitman (*Journ. of Morph.*, ii., p. 49). "Comparative embryology reminds us at every turn that the organism dominates cell-formation, using for the same purpose one, several, or many cells, massing its material, and directing its movements, and shaping its organs, as if cells did not exist." De Bary has summed up the matter in an aphorism: "Die Pflanze bildet Zellen, nicht die Zelle bildet Pflanzen."

of position to that of the hairs, spines, scales, and massive conical outgrowths well known upon the stems and cladode leaves of Ferns, though the details of structure are different. Since there is rarely any advance to photosynthetic structure in the dermal appendages of Ferns their comparison with microphylls in which it is a prevalent feature has been generally neglected. Nevertheless, that comparison is worthy of consideration from a broadly morphological point of view. An important feature which microphylls and dermal appendages possess in common is that they are normally sterile. In this they differ from the cladode-products of distal dichotomy.¹ It is hardly necessary to say that the parts thus compared are of widely homoplastic origin, as are also those progressions from hairs to broad scales, which have been traced in the dermal appendages of many distinct phyla of Ferns.² But the progression in Ferns habitually stops short at the protective spine or scale: none of their dermal appendages appear to have assumed an epidermis with stomata and mesophyll, nor yet a vascular supply, though occasional chlorophyll has been observed in them.³ The photosynthetic nutrition in Ferns is fully secured by specialised development of the cladode shoot that bears them.

A peculiar interest for comparison of living Ferns with early fossils lies in the stiff bristles and relatively large emergences present in certain Ferns of primitive type, and particularly on their stems and the bases of their leaves. The stiff "equisetoid" hairs of *Botryopteris* are, as regards cell-structure, only robust types of the simple hair. But in *Zygopteris* longitudinal cleavages of the lower cells produce a solid basal cone, or even a flattened scale.⁴ The former type compares with the stiff bristles, borne on a conical base and ending in a spine, which are found on the leaf-base and rhizome in some primitive Ferns, such as *Loxosoma* and *Dipteris*. They are structurally not unlike the simpler spines of the Psilophytales, though these habitually bear a distal gland, as in *Psilophyton princeps*.⁵ It is but a step further to the stiff branched hairs, each seated on a massive emergence, seen on the leaf-base of *Gleichenia pectinata* (Fig. 253). But the most notable of all are the chaffy scales of the Cyatheaceae, where the basal emergence is woody and persists, giving the characteristic "armature" of the stem and leaf-base (Fig. 430). These living examples are the result of enation from the leaf-base and the axis. At the growing point the scales may be associated with the young cladode leaves, from which they are distinguished by their number, arrangement, size, and structure (Figs. 255, 265 *bis*). In these features the modern emergences compare with the spinous appendages of the Psilophytales: neither the one nor the other is referable in origin to distal dichotomy.

The chief feature which appears to differentiate the dermal appendages of Ferns from the microphylls of other Pteridophytes is that the former take

¹ See Chapters XXIX, XXX.

² Bower, *Ferns*, vol. i., chap. xi.; also *Ann. of Bot.*, vol. xl., 1926, p. 479.

³ Hofmeister, *Higher Cryptogamia*, p. 212.

⁴ Holden, *Phil. Trans.*, B., vol. 218, p. 79, etc.

⁵ Lang, *l.c.*, 1932.

little or no part in nutrition, while the latter are usually photosynthetic. This difference is part of the functional make-up of the respective plants that bear them. In the Filicales the cladode leaves, originating by dichopodial branching, have habitually combined with it webbing, so as to form an efficient photosynthetic blade. Any further provision for this would seem needless, and the dermal appendages are protective, and only rarely



FIG. 430.

Young leaves of *Hemstelia grandifolia*, showing broad dermal scales borne on massive emergences, which persist as woody spines after the scales have fallen away : these give the "armature" frequent on the stems and leaf-stalks in Cyatheaceous Ferns.

contain chlorophyll. This result is seen in any normal Fern. But in many of the microphyllous types, such as the Lycopodiales and Sphenophyllales, the axes remain relatively slim, and their branches do not combine to form a specialised photosynthetic blade. The nutritive function is here relegated to the microphylls, or shared in various degree between them and the axes. In this the Articulatae often take a middle place : their microphylls sometimes assume a large share in nutrition, with vascular supply and even branching, as in *Archaeocalamites*, *Asterophyllites*, or *Annularia* ; while the axis serves mainly as a supporting and distributing organ. In the modern *Equisetum*,

however, the nutritive function falls chiefly on the tissues of the stem, notwithstanding that it never assumes the character of a webbed blade, and the leaves are scale-like. They are sometimes shed at maturity, as in *E. hiemale*, offering an analogy with the deciduous ramenta of Ferns.

The habitual allocation of photosynthesis in different types of Pteridophytes *either* to cladodes *or* to microphylls is not any sufficient reason for ruling morphologically apart those enations which are photosynthetic from those which are not. It is a recognised principle of morphology that relative position in the shoot-system takes precedence over functional specialisation. From this point of view the enation-leaves of the microphyllous Pteridophytes should be ranked with the spines, scales, and hairs of the Filicales, none of these being in the first instance of distal origin, as the cladodes are. But such grouping should be with that degree of looseness of allocation which naturally follows upon wide homoplastic origin. Interesting comparisons of habit may then follow, between the leaf-like expanse of the aerial shoot of a *Selaginella*, with its photosynthetic microphylls (Fig. 157), and the megaphyllous blade of a Fern-leaf, with its chaffy ramenta (Fig. 235). The superficial likeness is obvious enough ; as regards ultimate morphological analysis based upon development the correspondence between these is closer than some descriptive botanists would allow.

Lastly, there are certain positive features of organisation which microphylls and dermal appendages have in common. In neither of them is apical growth localised as it is in the cladode leaves of the Filicales. The relatively large size which some of them attain is due to intercalary activity, particularly in the basal region ; moreover, the distal tip frequently terminates in a hair, or it may be of a glandular character. Either of these is common in Ferns, and the same appears to have been a feature of the spines of certain Psilophytales (Fig. 425, *A*) ; moreover they are never normally fertile.

It may perhaps be thought that undue stress has been laid in the preceding pages upon the distinction between microphylls and megaphylls. Their origin, whether by distal forking or by enation, is certainly distinct in the most primitive forms ; but the subsequent transformation of the microphyll from an indeterminate growth to a bifacial photosynthetic organ with full equipment of ventilated mesophyll, stomata, and a conducting strand tends to level up the initial difference. In extreme cases the two types of leaf may be almost indistinguishable ; as, for instance, in the microphylls of Lycopods and the megaphylls of *Azolla*. On the other hand it may be argued that a distal forking is, after all, a form of enation, in which case the only difference would be one of position. There are few morphological distinctions which can be sharply and consistently drawn so as to meet all cases. The soundest position is to depend on early and on normal development. On this ground the initial distinction of microphylls and megaphylls would still hold for primitive plants, though liable to apparent obliteration in the later advances of the individual or of the race. As to the Higher Plants of the Land, it must be the task of a

later phase of Organography to decide how far the foliar organs in any given case are referable to one type or to the other ; or perhaps to some origin distinct from either. This cannot be done so long as the phyletic relations of the Pteridosperms, Gymnosperms, and Angiosperms remain as indefinite as they still are. Nevertheless, the adoption of the terms "microphyll" and "megaphyll" is held as justified for purposes of description of the Pteridophyta, and their use is based on the place of origin, and the mode of development of the parts connoted by them.

G. RELATION OF AXIS AND LEAF

The views thus expressed will necessarily affect conclusions as to the ultimate composition of the leafy shoot. At the opening of this Chapter reference was made to certain old methods of analysis of the shoot, from the point of view of phytonism ; and it was seen how the extreme view of Čelakovsky led him to a negation of the existence of an axis as an independent member. It was also noted that phytonic views are still entertained in some quarters, though now based upon comparison of plants lower in the scale. As against phytonic analysis in its most rigorous sense the recognition of the shoot as the fundamental unit was upheld, and now it remains to apply the distinction between megaphyllous and microphyllous leaves to the analysis of the shoot regarded as itself the morphological unit. The cladode and the enation-leaf differ in genetic relation to the shoot as a whole. The difference in initiation is a real one, as the state of *Asteroxylon* clearly shows. *The cladode would share a common origin with the axis.* The distinction of these parts being the consequence of dichopodial development of distal dichotomy, neither part would in the first instance pre-exist the other. But *the enation-leaf would have been from the first an appendage, borne laterally upon a pre-existent part.* In the former case the stem would be of the nature of a *pseudo-axis*, built up of successive parts referable theoretically to the bases of the successive cladodes. In this sense the stem as such would not have a separate existence ; moreover, this reference would be liable to be obscured and lost as soon as a lateral origin of the leaf-primordium followed as a consequence of advancing monopodial development. In the case of the microphylls the stem would have a theoretical existence as such, but it would tend to be obscured where their spread is extended towards apex and base. Such difficulties of interpretation are met by maintaining the recognition of the whole shoot, whether megaphyllous or microphyllous, as the morphological unit. After the initial steps, whether ontogenetic or evolutionary, are past it would be difficult or impossible to say, except in very primitive types, whether any given piece of stem was originally the indeterminate stalk of a dichopodium, or a part of a pre-existent axis which had produced monopodial leaves. Nevertheless, on the reasoning advanced above, the former is believed to have been its origin in the Filicales. It may be a question whether

or not the latter, with its pre-existent axis and minor appendages, will hold for all microphyllous types. It is quite possible that among the bizarre Devonian fossils so rapidly coming to light some may be found to yield on analysis of the shoot some intermediate or even some distinctively new type of foliar development.

So far then from contemplating a single original or ideal type of leaf, the tendency of the present time is to regard leaf-formation as a phenomenon which may have arisen in various ways, and have been often repeated in distinct evolutionary lines. It may even appear polyphyletically in the two alternating phases of the same plant ; for instance, in the prothallus and the sporophyte of *Equisetum*, or of *Lycopodium* : or two foliar types may appear nascent on the same phase, as in the dichopodially side-tracked cladodes, and the *Thursophyton*-leaves of *Asteroxylon* (Frontispiece). This attitude towards leaf-origin follows naturally from the recognition of size-relations as affecting primary growth. It may not be possible at present to determine the requisite numerical figures of proportion of surface to bulk for given examples, or to present the result as a demonstration of direct causality. But, written broad and large, leaf-development is an obvious means tending to uphold the proportion of surface to bulk in an enlarging organism. If that be so, then as an evolutionary proposition one ideal type of leaf would be out of the question.

CHAPTER XXVIII¹

THE CONDUCTING SYSTEM

THE Vascular Tissues provide the most constant structural characters of the plant-body; and, as they are naturally the best preserved features in the fossils, they give a basis for comparison between the ancient and the modern Pteridophytes. But in dealing with anatomical facts it must be remembered always that in any progressive evolution vascular structure follows and does not dictate form. All the evidence which it yields is necessarily *ex post facto* evidence. On the other hand, the structural effect of a certain development may persist after the formal characters with which it was primarily bound up have been altered, or even wholly removed. Anatomical characters are apt tardily to follow evolutionary progress, and thereafter to persist. They possess what may be described as a sort of phyletic inertia which gives them a special value in comparison.

The form which the primary conducting tracts take is related to the external form of the parts which they traverse. Since in most Pteridophytes they are clearly delimited from the tissues that surround them by an endodermal sheath this correspondence can be readily traced. For instance, a cylindrical root is usually traversed by a cylindrical stele; the stem likewise, though its stele is apt to be affected by leaf-insertion, especially where the leaves are relatively large. But the foliar trace is usually dorsiventral in accordance with the bifacial form of the leaf, and the same appears in minor degree in the pinnae and pinnules, though this relation is not always constant or exact. The correspondence may be maintained where the parts are small, and be continued through life in those plants or parts which do not grow to great size. But in those which attain large dimensions without secondary cambial activity various changes of form appear in the primary conducting tracts, which are not directly related to the external form of the part they traverse. These may be followed either by comparison of various types in the adult state, or they may be traced in the individual as it enlarges upwards. It has already been remarked that the normal primary form of a shoot, and particularly of the axis, is obconical, enlarging upwards. This is conspicuous in Ferns, and has been illustrated by Figs. 225, 266. Here the conducting tracts become more and more elaborate in form as the size increases, while the outline of the stem they traverse though enlarged is

¹ This Chapter is based upon *Size and Form in Plants*, Macmillan, 1930.

not materially altered. But if by starvation or some other cause the size is diminished a correlative simplification of the vascular system has been observed. There is thus a *size-relation* of the primary conducting tracts which appears to exercise a morphoplastic influence upon them. Their conformation does not run directly parallel with the external form of the part they traverse, but it is affected independently of it in accordance with the actual size. It is important to realise the fact that at least two independent influences are involved in the determination of the form of the primary conducting tracts, viz., relation to the external form of the part they serve, and a size-relation. A third influence, though not so important as it has often been assumed to be, is the insertion of the appendages with their individual vascular traces.

By a general consensus of opinion based on wide comparison the non-medullated monostele, or *protostele* as it is called, has been recognised as a fundamental stelar type for Vascular Plants at large, and particularly for the Pteridophytes. It is found in the latter that, however various the primary stelar structure may ultimately become, it is uniformly referable in origin to the solid cylindrical monostele. It is seen in the young sporeling to show either a solid woody core, or some vitalised or medullated state not far removed from it; and the former is retained in many relatively primitive Pteridophytes now living. A like structure is frequently present in the mature axis of early fossils; such observations show how fully justified that opinion is (Figs. 267-270). It is in long rhizomatous stems that the cylindrical protostelic state is most prominent, and in them its relation to the isolated leaf-insertions may best be studied in detail. There can be no doubt of the existence of the primary monostele in ordinary adult stems; but the real question is, how is it to be interpreted? Is the monostele an entity, forming an essentially "cauline" constituent of all axes; or is it a composite structure built up merely of "common" decurrent tracts from the leaves? Or does the truth lie between these extremes? In other words, may the stele encountered in the transverse section of an ordinary stem be partly common and partly cauline? An answer may be approached either by comparison of relatively primitive forms with those more advanced, or by following the details of ontogeny; but it cannot be assumed that the nature of the stele will necessarily be the same for all vascular plants, nor yet that every example will be open to such analysis.

Taking first megaphyllous types, as in the Ferns, the dichopodial origin of the shoot, by differentiation of an equal forking of a remote ancestry to form axis and cladode-leaf, has been recognised as being prefigured by the leafless Psilophytales.¹ Equal dichotomy in these has been figured in transverse section for *Rhynia* and *Hornea*²; and it is shown for *Asteroxylon* in Fig. 82, p. 119. But, in contrast to the last, illustrations with unequal forking

¹ Chapter XXII, p. 458.

² K. and L., i., Fig. 30, and ii., Fig. 42.

are shown by Kidston and Lang, the vascular supply of the smaller branch being caught on its way out through the cortex of the larger.¹ With these examples of equal and unequal forking in the Psilophytales, like conditions may be compared in *Botryopteris cylindrica* (Fig. 431, *A*, *B*). As a consequence of dichopodial development one shank of each unequal forking is seen

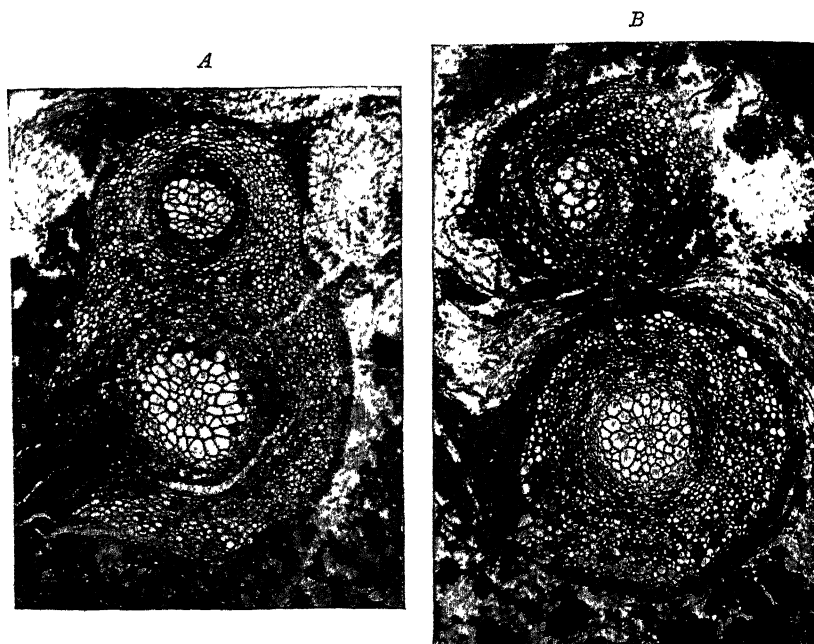


FIG. 431.

Botryopteris cylindrica. Form (*a*). *A* = Transverse section, showing unequal dichotomy. In the smaller branch the double protoxylem is very eccentric: in the larger branch there are three protoxylems. A root is being given off from this branch. *B* = Transverse section of stem and petiole. In the stem there are either two or three internal protoxylems. In the petiole there are two almost confluent, on the lower (originally adaxial) side of the bundle. In both specimens the outer cortex is almost lost. \times about 24. (After Scott, S. Coll., 1906.) (From photographs by Mr. W. Tams.)

in either case to be side-tracked, and its trace would be laterally inserted on that of the relatively larger strand. If the former were developed as a leaf and styled as such while the latter were the relative axis, the stele below the entry of the trace would be composed partly of "cauline," partly of "common" vascular tissue; but above the insertion the "cauline" tract alone would be continued to a later forking (*B*). The same may be seen in *Cheiropleuria*, as an example of those Ferns where the rhizome of the adult is elongated and forked. Here the disproportion in size between the stele and the leaf-trace is great (Fig. 269). The stele may be followed up to the apical cone itself, as a column of procambium maintaining its identity, while giving off successive

¹ K. and L., iii., Pl. xi., Figs. 83, 84.

fractions of its tissue, as the leaf-trace to each isolated leaf. The residual vascular tissue appears to be truly cauline, and not referable in origin to leaf-trace tissue. From the dichopodial point of view this would represent the vascular supply to the stronger axial shank, which is capable of continued apical growth and further forking.

Turning now to the embryology of the megaphyllous type, the dichopodial theory has been applied to that of the Leptosporangiate Ferns in Chapters XXVI, p. 534, and XXVII, p. 550; the result, based on comparison with forked embryos of *Tmesipteris*, is that the Fern embryo may be conceived as presenting a very early dichotomy to form axis and cotyledon, but with the foliar shank precociously advanced, while the axis, with its powers of further dichopodial branching, is delayed (Figs. 417, 419). In ordinary embryos at this stage the stem forms no vascular tissue of its own comparable with the cauline tract of *Botryopteris* or *Cheiropleuria*. This may be held as being in abeyance, in relation to the delayed development of the axis, and in accordance with the precocious rush of the first leaf. The same may hold for succeeding leaves also, until the adult state is reached. The adult shoot of the Filicales fluctuates between a preponderance of leaf over axis and a reasonable balance between the two. In the former the vascular system may appear as though made up exclusively from leaf-traces; in the latter, at a varying stage of the ontogeny, a coherent body of vascular tissue, partly made up of elements which have a truly cauline origin, serves to connect up adjacent leaf-traces.¹ The greater the preponderance of the leaf over the axis in the young shoot the later will be the stage when this composite nature of the stele can be recognised. Thus far the anatomy accords with a dichopodial theory of origin of the shoot in Megaphyllous Pteridophytes.

In the Microphyllous types the composite nature of the adult stele is more obvious. For instance, in *Lycopodium* the stelar column can be traced up to the apical cone, beyond the insertions of the youngest leaves: it is thus mainly of cauline nature, and the relatively small leaf-trace-strands are inserted upon it with a minimum of local disturbance (Figs. 166, 167). In *Asteroxylon*, *Psilotum*, and *Tmesipteris*, which all possess microphyllous leaves, the basal region of the plant is leafless, and there the cylindrical stele is necessarily cauline. Even in the leafy region the cauline stele is still the dominant factor: for the minute vascular twigs given off from it often end in the cortex, though sometimes they may enter the appendages, particularly in *Tmesipteris* and *Arthrostigma*. Thus it is seen that the monostele of the microphyllous Pteridophyta may be purely cauline in structure in the simplest types. But in those which are more complex it is a composite body, the proportion of cauline and common tissue varying according to the relative

¹ Campbell, *The Eusporangiateae*, p. 174; West, *Ann. of Bot.*, 1917, p. 369; Bower, *Ferns*, vol. i., p. 139.

preponderance of axis or of leaf. In the simplest megaphyllous forms, on the other hand, the monostele is a composite body although its components will have had a common axial origin. In more advanced forms the proportion of cauline and common tissue will vary as in the microphyllous types. Nevertheless, for purposes of description and comparison the monostele of both types may be held as a unit. Adhering as before to an upward view in comparison, the conclusion follows that the protostele represents a primitive conducting tract, as seen in simple form in the Rhyniaceae. Where appendages, whether microphylls or megaphylls, appear as dominant features of the shoot their vascular supply may supersede in varying degree, or even eliminate the cauline protostele. But all such happenings are in the nature of amendments upon an originally simple plan. It thus appears that the vascular anatomy of the Pteridophytes accords with the external organisation of their shoots, whether megaphyllous or microphyllous, *up to a point; but the Form of the vascular tracts cannot be wholly explained in this way. A moulding influence in relation to Size requires also to be taken into account as leading to the final result, particularly where primary tissues only are involved.*

THEORY OF SIZE

The relation of Form in Plants to their actual Size, and particularly the changes of contour which follow on its increase, has already been noted in the foregoing Chapters. Since the most striking examples of that relation are found in the primary vascular tracts of Primitive Plants, this Chapter, which deals comparatively with their conducting system, seems to be the most fitting place for introducing a brief statement of the Theory of Size and Form.

The Principle of Similarity, first enunciated by Galileo, reigns supreme over all structures, whether unorganised as in buildings and the engineering works of man, or organised as in animals or plants. Its mechanical application affects stability and strength; its physiological application in the living organism works out through the proportion of any limiting surface to the bulk of the tissues enclosed by it. As the size increases the strength of a structure increases as the square of the linear dimensions, but the weight or mass as the cube, provided the form and material remain the same; further, in similar solid figures whatever their form, provided that on enlargement the same form be maintained, the surface increases as the square, and the bulk or volume as the cube of the linear dimensions.

From the time of Stephen Hales this principle has been widely illustrated in its application to the bodies of animals, and many of their peculiarities of form and structure have been recognised as necessary consequences of its effect in the course of their evolution. Botanists have, however, been slower in applying the Principle of Similarity to the study of plants. It is true that the question of the practicable limit of the height of trees has long ago been discussed from this point of view, and it has been recognised that a change, either of material or of the method of construction, would be

necessary for effective growth beyond the limits already reached by some of the largest of them. In fact 300 feet or rather more is the extreme height that can be self-supporting with the usual construction of the woody trunk; and that is the approximate level of the highest canopy in tropical forests.

The incidence of a mechanical limit is, however, only one way in which the Principle of Similarity applies to living organisms. A much more intimate and far-reaching influence of the size-factor on their construction arises from progressive change in the proportion of surface to bulk in growing cells, tissues, or parts. The importance of this lies in the fact that physiological interchange, which is inseparable from active life, is conducted through limiting surfaces, external or internal. It may be assumed that, other things being equal, and where the surface is continuous and unbroken, such interchange will be directly proportional to the area of surface involved. But if the form be maintained unchanged in a growing cell, tissue, or part, according to the Principle of Similarity while the bulk increases as the cube of the linear dimensions, the surface increases only as the square. Hence there would be a constantly decreasing proportion of surface to bulk, and as constantly an approach to a point of physiological inefficiency. On the other hand, any change from a simple form, such as a sphere or cylinder or cone, which gives a more complicated outline will increase the proportion of surface to bulk; for instance, corrugation or fluting of the surface, or branching and segregation into parts; and the same applies also for bodies of more elaborate form than those named. Thus increasing morphological complexity involving any increased complication of form would tend to meet the physiological need consequent on increasing size, by levelling up the proportion of surface to bulk.

In the construction of any ordinary Vascular Plant there are three limiting tissue-surfaces of prime importance: (i) the outer contour of the plant or part, complicated though it usually is in sub-aerial plants by the added cell-surfaces lining the ventilating channels; (ii) the endodermal sheath, which delimits the conducting tracts from the tissues that envelop them; and (iii) the collective surface by which the dead tracheal system faces the living tissues that surround or permeate it. Each of the three is a surface of physiological transit, and each independently of the others will be a suitable subject of observation from the point of view of the proportion of surface to bulk as the size increases. Of these the third is the most important in the comparative study of form in the conducting tracts of the Pteridophyta: for the woody tissues are those best preserved in the fossils, and being resistant they frequently retain their natural outlines, and make it possible to contrast their form and dimensions with the corresponding tissues in their living correlatives. We may then expect that in the smallest, and particularly in their sporeling stage, the form of the conducting tracts will be simple, such as the cylinder. Moreover, this is frequently continued to the adult state in the most primitive Pteridophytes. But with greater size its form tends to become more complicated, as it is seen to do even in the progressive stages of the individual life (Fig. 266). The primary conducting tracts of the Pteridophyta offer the best examples of moulding in accordance with the Principle as above stated.

STEMS

A very primitive type of protostele is seen in the leafless fossils *Hornea* and *Rhynia major*, where its form is cylindrical, and it lies centrally in the circular section of the shoot (Fig. 80). The stele is clearly marked off from the inner cortex, but without a definite boundary; peripherally there is a wide zone of phloem surrounding the central solid core of wood: in the latter a distinction is seen between inner and outer tracheides (Fig. 432). There is an essential likeness between this and the protostele of *Botryopteris* (Fig. 267), or that of the living Fern *Cheiropleuria* (Fig. 269). These steles are all of primary construction. That of *Rhynia* is relatively small, being about .5 mm. in diameter. But those of related living plants such as *Psilotum* and *Tmesipteris* are larger, and they are seen to increase in size upwards as the plant develops, assuming the usual obconical form. Thus the plant as a whole, and the woody core in particular, is gradually brought up against that difficulty of proportion of surface to bulk which necessarily follows on enlargement, if the original form be maintained. The natural resource is a change of form or of constitution, or of both. A primitive change of form has been to adopt the fluted column in place of the cylinder, and the more numerous and deeper the flutings the greater the effect. The following table shows the relation of their number to the increasing diameter of the xylem in certain fossil protosteles:

Name.	Diameter in mm.	Description of Form.
<i>Hornea</i> (K. and L.) - - -	.3	Cylindrical
<i>Rhynia major</i> (K. and L.) - -	.5	"
<i>Asterox. Mackiei</i> (K. and L.) -	1.8	Stellate: 4 rays.
" <i>Elberfeldense</i> (K. and W.)	2.2	" 10 "
<i>Cladoxylon</i> (K. and W.) - -	2.25	" 10 "
" "	3.7	" 25 "

In all of these the woody core is a solid mass of tracheids, though tending towards disintegration in the largest. They illustrate the change from a cylinder to a fluted column as the size increases; while the number of the flanges rises, though not in any exact ratio to the diameter. A similar relation of size and form is seen in the steles of certain fossil Ferns (Fig. 268), though here the flutings show increasing depth rather than number in the larger types. Such facts indicate that the adjustment is not restricted to one phylum: nor is it dependent upon leaf-insertion, for in both *Asteroxylon* and *Asterochlaena* the small leaf-traces are affixed upon the flanges irregularly as to number and position. A flanged stele may also be present in the leafless rhizomes of *Psilotum*, where again they show a relation of number to size (Fig. 88); or in the leafless stolons of the living Fern, *Nephrolepis*. The

general conclusion will be that *the flanged adjustment* is determined, whether in depth or in number of the flanges, in relation to size, by some inner impulse, and *may be independent of leaf-insertion*.

The Lycopodiales present on the one hand gigantic fossils, on the other relatively small survivors of the present day. But the vascular system in them all is referable to the initial protostele with a solid tracheidal core, and it is little affected by the insertion of the traces of the microphyllous leaves. Naturally the ontogenetic evidence is imperfect for the fossils, though it is available for the living types; nevertheless there is no doubt that the

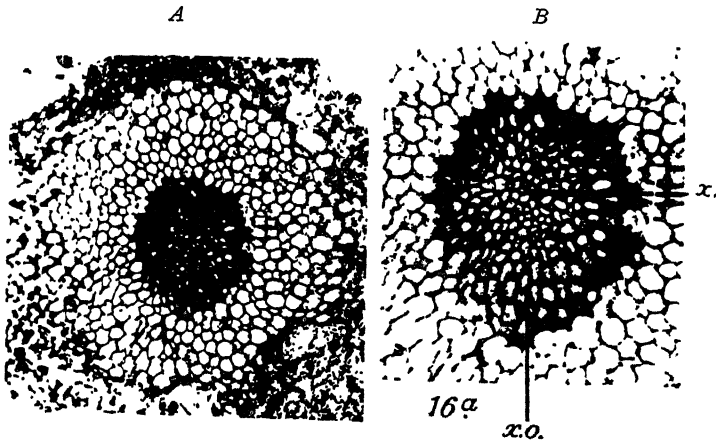


FIG. 432.

Rhynia major. A=Transverse section of stele showing xylem-core, and phloem. B=Central portion of the same, showing details of the xylem; x.o.=outer xylem; x.i.=central xylem. A $\times 33$; B $\times 60$. (After Kidston and Lang.)

cylindrical protostele was the starting-point for both. In the fossils the modifications on the primitive xylic column, as the size increases, consist in (i) *fluting* of its surface, as shown in the "corona" of certain types (Fig. 174), the shallow flanges appearing as features of the stele itself independent of the leaf-insertions; (ii) *medullation*, sometimes with its intermediate stage of "mixed pith" (Fig. 176): it is a feature in most fossil Lycopods, and the pith may occupy a large proportion of the core; (iii) *cambial increase* forming a secondary zone of wood "vitalised" by medullary rays (Fig. 177, x_2); and (iv), in some species of *Sigillaria*, *segregation* into separate strands of that vestigial ring of the primary xylem which survives from advanced medullation (Fig. 177, x). Each of these four methods of elaboration helps towards levelling up the proportion of that collective surface by which the mass of tracheidal wood forms contact with living cells. The effect of all four in combination, as in the Permian *Sigillarias*, is cumulative. Nevertheless, all these plants are extinct. The fact suggests that, even with such modifications of form as these, the purely tracheidal primary wood has proved one of

Nature's failures where the size is large. This increases the interest in those living forms, where the primary wood is purely tracheidal though their size is relatively small.

In the living species of *Lycopodium* the method of adjustment to increase in size of the wood within the cylindrical stele is essentially the same as that of the fluted column, though differing in detail. As the stele enlarges the peripheral protoxylems increase in number by splitting, while the phloem intrudes into the deepening grooves between them. The appearance in transverse section is as of disintegration of the wood into separate tracts. But, in fact, the wood is all connected upwards and downwards into a *xylem-sponge* (Fig. 168). The effect, in respect of surface-exposure of the purely tracheidal wood to the living tissue around it, is the same as that in the less efficient methods of the related fossils. But the living Lycopods have the advantage in possessing a method automatically adjustable as the size increases. Nevertheless, though they survive, none of them approach the dimensions of the dead fossils. Here again, excepting in the smallest, the moulding of the wood is independent of leaf-insertion.

The extraordinary adaptability of the stele in *Selaginella* according to increasing size has been discussed in Chapter XII. Here it must suffice to state that its wood is again purely tracheidal, that the chief method of maintaining its presentation-surface is by elaboration of the ribbon-form of the protostele, and that the changes are again independent of leaf-insertion. But frequently the stele as a whole with its delimiting endodermis partakes in further plastic changes, and the stem becomes polystelic (Fig. 171). Lastly, in the rhizomes of certain species belonging to different sections of the genus (*S. Lyallii*, *uliginosa*) the moulding of the stele is of the same type as that prevalent in Leptosporangiate Ferns, viz., *solenostelic* (Fig. 172). In plants so different as these—the one type microphyllous, the other megaphyllous—the origin of the same feature must have been homoplastic. The solenostelic state is regarded in both as a method of maintaining the presentation-surface as size increases, whether of the xylem only (solenoxyllic), or of the second limiting surface also, viz., the endodermis, giving full solenostely. A high degree of resource is thus shown by the Lycopodiales in moulding their conducting tracts in accordance with the demands of increasing size. But in common with most primitive vascular plants they retain the purely tracheidal wood, without its permeation by living parenchyma. This feature retained by the living Club Mosses may probably account for the variety of the methods adopted; and particularly by *Selaginella*, which in point of number of species and of spread has been the most successful of them all. Most plants with purely tracheidal wood are extinct, and none of the survivors have attained large size. Death or a stunted existence seems to have been the consequence of their conservatism. The largest of the survivors that fully retain that disability appear to be the ancient Family of Osmundaceae

Ferns, which date from the Permian Period. We conclude that the mere enlargement, even with complicated moulding, of a tract of dead tracheides does not suffice to meet the demands of modern life, except on a small scale. The wood of modern forms, and particularly that of the Ferns, is almost always “*vitalised*” by the presence of living parenchyma intimately associated with the tracheids (Fig. 274).

It is in the megaphyllous Ferns that the primary vascular tracts are moulded to the highest complexity. Cambial thickening is rarely present in them, though it is seen in the living *Ophioglossum*, and in such early fossils as *Botrychioxylon*; but it never became a confirmed feature in Ferns. Elaborate moulding of the enlarging primary tracts may be held as a physiological set-off to the absence of this more direct way of meeting the demands of increasing size. It has been seen how in some of the ancient and chiefly microphyllous types an adjustment of form by fluting of the xylem, or of the whole stelar column, may have sufficed. But in the megaphyllous Ferns, and particularly in the modern Leptosporangiates, the whole stele with its phloem and endodermis shares in the changes of form that are adopted, as the individual passes from the sporeling to the adult state. The final result may then be not merely an internal adjustment of the monostele, but that state which is described as “*polystelic*.” Examples have been described in Chapter XVII, and are illustrated for modern Ferns in Figs. 266-280. But this condition had already been attained in its most complex form by the Permian fossils of the genus *Psaronius*; though here its origin must have been homoplastic with that of the Leptosporangiate Ferns.

The elaborations of the stele with increasing size as seen in Leptosporangiate Ferns all centre round the *solenostele*. The stele of the sporeling is typically protostelic; hence the origin even of the most elaborate states may be traced ontogenetically, and this will be most readily done in some rhizomatous Fern, where the intervals between the leaves are long: such as *Gleichenia pectinata*,

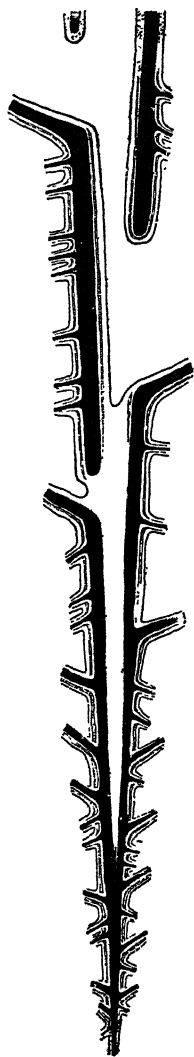


FIG. 433.

Plan of the stelar construction of a young plant of *Gleichenia pectinata*, after Dr. J. McL. Thompson. It shows in median section the way in which the stele enlarges comically upwards, and widens into a solenostele with leaf-gaps.

or *Loxsonia*. The form of the adult solenostele is a hollow cylinder surrounding a central pith, which is in communication with the external cortex through the foliar gaps, of which one marks the point of departure of each leaf-trace (Fig. 275). The cylinder

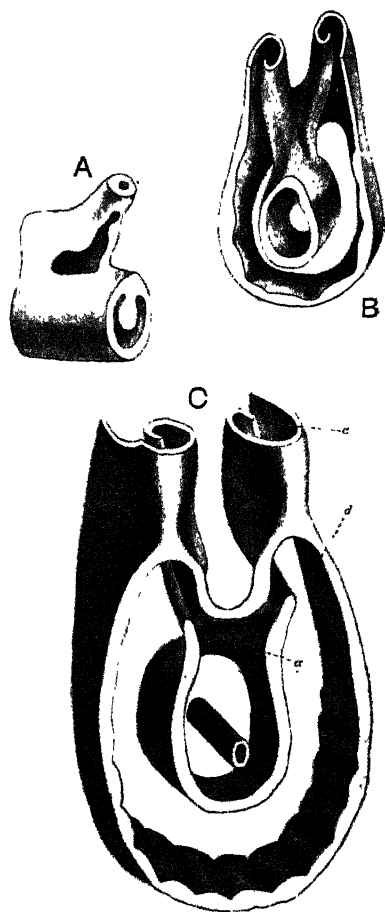


FIG. 434.

Drawings from wax models of the stellar system of *Matonia pectinata*. A = from a young stem showing a node. B = from an older stem showing a node seen from behind. C = a still older node seen from in front. A $\times 25$; B $\times 12$; C $\times 10$. (After Tansley and Lulham.)

consists of a tube of xylem surrounded inside and outside by continuous phloem, and bounded by a continuous sheath of endodermis. Its complete enclosure within and without by this is a matter of physiological importance, and the problem will have been to derive this elaborated stele of the adult from the protostele of the sporeling without any break of that continuity. The danger points of leakage would be at the departure of each leaf-trace from the primary stele, and at the point of transition from solenoxyle to full solenostely; but particularly the latter. The structural steps may be followed in the reconstruction by Dr. J. McL. Thompson in Fig. 433. The sporeling starts from a stele having a solid xylem-core, which soon becomes medullated. Later the enlarging pith is surrounded by internal phloem, a stage which in a contracted form is permanently retained by the type of stele seen in the adult stem of *Lindsaya*; but in the allied genus *Odontosoria* and in *Gleichenia pectinata* solenostely follows. First a series of successively deepening axillary pockets are formed by apparent involution of the endodermis; then a sudden structural change takes place, the endodermis being continued across the whole width of the pith, thus cutting off the

intrastelar region that lies below it from that which is above: the latter is now continuous with the cortex. From this point onwards the central tract of the pith becomes physiologically extra-stelar, though in the ontogeny the part below the barrier was intra-stelar. This sudden structural change is opportunist in character rather than morphologically consistent. It may be

held as justified by the functional advantages that follow from it. In the first place, the change is effected without any breach of continuity of the endodermis. Secondly, the solenostely thus established allows of a common ventilation-system extending from the cortex through the foliar gaps to the central column, which is geographically intra-stelar but now physiologically extra-stelar. Thirdly, it completes the doubling of the surface-presentment of the stelar tract to the ventilated parenchyma, so important as the size increases : for the solenostele now has endodermis on both sides. Moreover, by enlargement of the stelar ring, which is a marked feature as a rule so soon as the solenostele is established, the xylic ring can be thinned out, sometimes to a single row of tracheids, so as to give high surface-presentment of the tracheids to living cells. Such considerations suggest that in that puzzling structure, the solenostele, we see a biological adjustment which makes increasing size functionally easy for a primary conducting tract completely enclosed by endodermis. A like argument, *mutatis mutandis*, will apply to the homoplastic solenostely of *Selaginella*, which, however, is microphyllous : a fact which suggests that solenostely is a phenomenon of purely stelar adjustment.

Once solenostely is established in the stem, all further mouldings connoted by dictyostely (Fig. 277), polycycly (Figs. 278, 434), and perforation (Fig. 280) simply elaborate the scheme thus initiated. As an extreme example of the complications which the stelar development in Ferns may attain, the fossil *Psaronius infaustus*, with a stelar system 64 mm. in diameter, has been diagrammatised by Hirmer as consisting of twelve concentric cycles.¹

Following out these lines of probable evolutionary progress, and particularly as presented by the Leptosporangiate Ferns, a general tendency is seen towards an increasing disintegration of the conducting tracts in the stem. Its progress is doubtless in great measure dependent on increasing size ; but this will not fully explain the facts. A comparison of the instances shown in Fig. 278 indicates that the relation between size and disintegration is not always obligatory, or indeed close. The consequences of disintegration are not only increase of presentation-surface, but it brings also enhanced facility for gaseous interchange between the central parenchyma and the cortex ; and onward through pneumathodes with the outer air. Structural modifications that secure such ends form part of that adaptive advance which characterises a higher state of evolution, but carried out under the restricting absence of cambial increase. Comparatively the increase in number and size of the perforations seen in the more advanced Leptosporangiate Ferns is held as one of the marks of this advance : and the resulting disintegration has been used as one of the criteria of comparison in their systematic grouping.²

¹ *Handbuch der Paläobotanik*, Fig. 680.

² *Ferns*, vol. i., chap. viii., and especially p. 159. Hayata has recently analysed the adult polycyclic stems of *Angiopteris*, *Saccoloma*, and *Thyrsopteris*, after the

The establishment of solenostely itself bears a general though not an exact relation to size. Indications of this may be traced in the individual by measurement of successive transverse sections through the basal region, including the zone of the transition; for instance in *Loxsoma*, and in *Gleichenia pectinata*, which are both rhizomatous but of no near affinity:

Name.	Diameter of Stele in mm.	State.
<i>Loxsoma cunninghami</i> -	.4 .8 1.7	Protostelic <i>Lindsaya</i> -stage Solenostelic
<i>Gleichenia pectinata</i> -	.85 1.0 1.5	Protostelic Central pith Solenostelic

The structural progression in both is of the same order, though the figures do not coincide. There is, in fact, a somewhat wide range of variability as to the incidence of solenostely in relation to size. Occasionally a fluctuating structure is seen with recurrently imperfect solenostely, as in *Platyzoma* (Fig. 271). In this as well as in normal examples a diameter of about 1.0 mm. appears to be a critical size of stele, about which solenostely is completely established. In other Ferns it may be larger or smaller; in the microphyllous *Selaginella Lyallii*, however, a complete solenostele may appear with a stelar diameter of only .5 mm. (Fig. 172). On the other hand, an interesting comparison of a number of species of the *Lindsaya-Odontosoria* affinity shows that in them the *Lindsaya*-structure is present below 1.0 mm. diameter; but above that the characteristic solenostele of *Odontosoria* appears. This again points to a diameter of 1.0 mm. as critical, a conclusion which accords with the figures in the above table.¹

LEAVES

The vascular supply of the microphylls presents few points of interest, once the entry of the strand into the leaf is established. In the great majority of them it remains minute and simple: though occasionally it may separate more or less completely into two parallel strands, as in *Sigillariopsis*²; but

manner of a Fir-Cone made up of wedges, of which each base represents part of the outer surface. This method deals with elaborate adult structure. The results are interesting, but they cannot bear the same evolutionary significance as those of the ontogenetic study onwards from the protostelic sporeling. ("Neue Keiltheorie z. Erkl. d. Konstrukt. d. polyzyklischen Stelen," *Ber. d. d. Bot. Ges.*, Bd. xlix., 1931, Heft i.)

¹ For further details see *Size and Form*, chaps. vii., viii.

² Scott, *Studies*, vol. i., Fig. 101.

those strands fuse again distally. It is true that the leaves themselves dichotomise in *Asterocalamites* (Fig. 125), in *Protolepidodendron*, and in *Sphenophyllum* (Figs. 105, 111); in the last the leaf-segments may even be webbed into an expanded blade, suggesting Fern-like characters.¹ But the existence of dichotomy and webbing is too slender a basis on which to found a relationship between Classes otherwise so remote. In the Calamarians also forkings may occur, particularly in the bracts of the fertile cone. But in all such cases the leaf-trace remains simple.

The megaphylls, theoretically equivalent in ultimate origin to the axis that bears them, present features which uphold that source, though as their size increases their vascular supply has pursued an independent course in relation to the prevalent dorsiventrality. But this is not so marked a feature in early fossils as in the leaves of later date. For instance, the leaves of *Botryopteris* (Fig. 281), or of *Thamnopteris* (Fig. 282), or of the Zygopterids (Fig. 283) all show at the extreme base a coherent meristele, structurally comparable with the stele of the stem except for a tendency to dorsiventrality. This accords with the theory of the dichopodial origin of the cladode leaf. But the elaboration of the petiolar meristele upwards has followed lines of its own in relation to size.

The origin of the petiolar meristele, typical for Ferns generally, has been referred by Gwynne-Vaughan to a simple vascular tract such as is seen in the leaf-trace of *Thamnopteris* (Fig. 282). It has been described in Chapter XVII; but the main features may be briefly restated here. The meristele, originally protostelic and oval in section with a single mesarch protoxylem (Fig. 282, 1, 2), soon opens on the adaxial side, exposing the protoxylem (3, 4); the bay thus formed widens, and a channelled though coherent strap of xylem results (5-7); its margins curve inwards so as to give the characteristic horse-shoe outline in transverse section. This change is accompanied by great lateral expansion, the nature of which (though not the proportion) appears in the later figures of the series. The actual proportions as derived from meristeles all drawn from the same shoot are presented natural size in Fig. 435. If the largest of these were flattened out it would be found to measure about 18 times the width of the first. A like increase in width is seen in modern Osmundaceous Ferns. Meanwhile the protoxylems multiply by fission, and are ranged along the adaxial side, the whole being enclosed together with the phloem by endodermis. Thus a normal petiolar trace may be derived upwards from a type little differing from an axial protostele at the extreme base.²

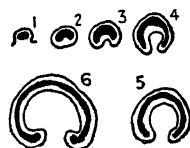


Fig. 435.

Meristeles of *Thamnopteris* traced from the type specimen, showing the actual dimensions as the trace passes outwards into the leaf-base. The adaxial side faces downwards.

¹ Lignier, *Bull. Soc. Linn. de Normandie*, Caen, 1903.

² Kidston and Gwynne-Vaughan, *Proc. R.S. Edin.*, 1908, p. 433.

This ribbon-like form of the foliar meristele in Ferns brings a double advantage: it makes conduction to the margins of the dorsiventral leaf easier, while the form assumed is such as to tend to maintain the proportion of surface to bulk of the conducting tract, and especially of the xylem, as the size of the part increases. Here also, as in the solenostele, the wood may thin down in high degree, as shown in the large meristele of *Metaxya* (Fig. 285, 3). The usual gutter-like form, giving a horse-shoe curve in section, is liable to considerable variation. But, it may be asked, why should a gutter-like form be assumed at all? Probably there may not have been only one determining cause, but a potent factor has been that, while securing by its flattened form a levelling up of the proportion of surface to bulk as the size increases, the widening ribbon in this way adjusts itself within the ring of a firm resistant rind (Fig. 436, *A*, *B*). But if this were a determining reason for the channelled

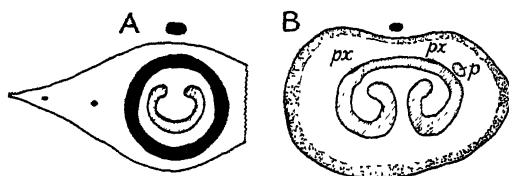


FIG. 436.

Diagrammatic drawings of transverse sections of petioles. *A*—leaf-base of *Osmundites* *Kolbei*, after Kidston and Gwynne-Vaughan, showing adaxially curved meristele within a sclerotic ring. *B*—*Anachoropteris rotundata*, after Scott, showing abaxially curved meristele; the width of the stelar ribbon is to the diameter of the petiole as 12 to 8. *px*=protoxylem; *p*=pinna trace. The black dot indicates for each the direction of the axis.

form, would it not be possible that the concavity might be either adaxial or abaxial? As a matter of fact both exist: the former appears constant in living Ferns (*A*), but certain early fossils grouped as the "Inversicatenales" illustrate the latter. For instance, in *Anachoropteris* not only is the curvature reversed, the concavity being abaxial, but also the insertion of the pinna-traces has slipped from the margin to a position on the adaxial face of the meristele, though in the Leptosporangiate Ferns it is on the abaxial face (Fig. 436, *B*). All this is intelligible in a widening meristelar strap, and it is obviously related to the dorsiventrality of the blade.

A parallel may not inaptly be drawn between the vascular supply of a primitive Fern leaf, such as *Osmundites* (Fig. 436, *A*), and the shoot of a large dorsiventral species of *Selaginella* (Fig. 171), where also there is at the base a widening ribbon within a firm rind. In *S. Willdenovii* the widening stele becomes convoluted within its resistant barrier. At the base it is oval, with a ribbon-shaped xylem (1): the margins of the widening strap curl irregularly inwards, but the continuous strap is here broken up, and by endodermal involutions the parts are separated as a plurality of meristeles (5-9). If, however, the widths of these isolated stelar ribbons be added together, as they might be if placed margin to margin, their sum would be greater than the widest diameter of the oval section. In a given case the ratio

of the five meristemes to the diameter of the whole stem was found to be 1.64 to 1.0. The polystely in *S. Willdenovii* is, in fact, another way of packing a widened ribbon within a resistant rind, and in this it is comparable with the channelled meristeme of the Osmundaceae, or of *Anachoropteris*.

As pointed out in Chapter XVII the widening out upwards of a narrow strand into a sheet of conducting tissue, such as that in Osmundaceous petioles, would have the effect of leaving the narrow base of insertion on the axial stele functionally as an undesirable bottle-neck. The Osmundaceae have retained this archaic disability to the present day. But in many more advanced Ferns, particularly in the solenostelic types, the base of insertion of the meristeme has itself widened, so that it involves a considerable sector of the stele. This change has been quoted as illustrating that tendency to basipetal phylogenetic development to which Tansley drew attention in his *Lectures on the Filicinean Vascular System*.¹ He concluded that the evolution of the leaf itself is the main determining factor in the changes occurring in the vegetative body: he recognised a tendency to carry down the widened C-shaped structure to the point of junction with the stele of the rhizome. From this point of view, through the formation of an axillary pocket, the evolution of the solenostele itself seemed to depend primarily on such basipetal evolution. Tansley's Lectures were published before the ontogenetic development of the solenostele in such Ferns as *Loxosoma* or *Gleichenia pectinata* had been actually observed. There can be little doubt that the evolution of the leaf has exercised an important influence in determining the final result; but ontogenetically the formation of an internal pith and even of an internal phloem in the obconical axis precedes the advent of full solenostely in the examples named; while the solenostele is finally completed structurally by the extension of the endodermis across the whole width of the pith (Fig. 433). The expression "basipetal influence" of the leaf appears to be an inverted way of expressing the changes consequent on upward expansion of the whole shoot, in which the demands of a size-relation make themselves apparent in the structure that follows. The one view expresses the result of enquiry in passing downwards from the adult to the sporeling: the other the result of a converse enquiry directed upwards from the sporeling to the adult. The latter follows the ontogenetic story, and is probably the more natural and true. But whatever view be held for Ferns, solenostely in the microphyllous *Selaginellas*, or at the base of the leafless runners of *Nephrolepis*, cannot be ascribed to any downward influence from the leaf. We conclude that solenostely is a consequence of increasing size upwards, and the widening of the base of the foliar meristeme is correlated with it.

Mere widening of the foliar meristeme results in a continuous sheet of vascular tissue, which together with its endodermis constitutes a barrier to gaseous interchange (Fig. 437). This physiological difficulty has been dis-

¹ *New Phyt.*, Reprints, No. 2, p. 53, 1908.

cussed in Chapter XVII, together with the means by which it has been met ; viz., by " perforations " related in number and position to the size of the meristele, and particularly to the opportunities for ventilation to the outer surface by means of pneumathodes. Relatively primitive types, such as *Dipteris conjugata*, *Metaxya* and *Pteris podophylla*, have retained this disability of a continuous meristellar sheet. Disintegration of the meristele by one or more perforations according to the size is the natural remedy, and this has been held as a feature of morphological advance : it is present in many Leptosporangiate Ferns (p. 346, Figs. 285-289). On the other hand, it has also been shown in Chapter XVII that the origin of the pinna-traces in simple cases is from the margin of the flattened meristele ; for instance, in

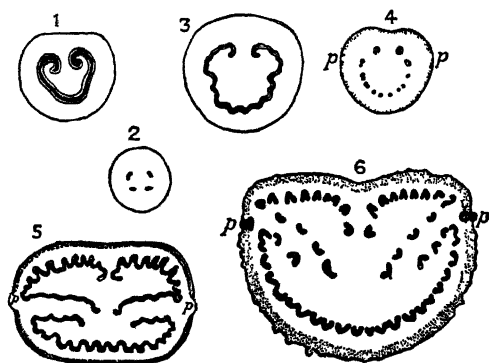


FIG. 437.

Transverse sections of petioles, all drawn to the same scale ($\times 2$). 1, *Dipteris conjugata*; 2, *Dipteris Lobbiana*; 3, *Metaxya*; 4, *Phlebodium aureum*; 5, *Thyrsopteris*; 6, *Alsophila*. These show that while greater size leads to vascular disintegration, there is no definite proportion. *p* indicates the position of the pneumatophores.

Schizaea, or in *Pteris umbrosa* (Fig. 289). But where the meristele is wide and curved their origin is "extra-marginal," or better described as "superficial." Where it is thin the departure may cause a "pinna-gap," comparable with the foliar-gap from a solenostele. Illustrations of this appear in *Lophosoria* (Fig. 291), and in *Botrychium* (*Ferns*, Vol. II., Fig. 360). In Leptosporangiate Ferns the superficial pinna-trace originates normally on the convex abaxial face of the meristele ; but in the Inversicatenales the abaxial surface is concave, and the adaxial convex ; and the pinna-trace then springs from the latter (Fig. 436, *B*). The fact is that the point of attachment of the subsidiary part to the parent vascular tract is not uniform, but adjustable in relation to its margin. The chief interest in these facts lies in the parallel between the vascular features of the axis and those of the cladode leaf. They show that, in the detail of their connections, as the stele of the stem is to the meristele of the leaf so is the meristele to the pinna-trace. The foliar-gap corresponds to the pinna-gap, while both of these are distinct in nature and in origin from those perforations which appear, independently of the traces,

both in the solenosteles and in the meristeles of advanced types. The principle which appears to determine the place of attachment of the subsidiary to the parent tract is to secure that, whatever the curvature of the latter, the subsidiary supply shall spring from the available spot nearest to the base of the part which it serves.¹ On the other hand, the *rationale* of the perforations, whether of the solenostele or of the meristele, is to secure free physiological passage through a sheet of tissue otherwise impervious. These comparisons between axes and cladode leaves may be held as supporting the cladode theory of the origin of those parts from a common source. Further, the behaviour of the whole vascular system of the leaves of Ferns as their size increases is analogous to that of a dorsiventral shoot of one of the larger Selaginellas, which is also of cladode origin. In both the conducting tracts pursue a course so far alike as to give added support to the cladode theory. Both are ultimately referable to a dorsiventral development of a dichopodial system.

There is no need to do more than mention here the venation of Fern leaves, already described in Chapter XVII. The primary venation is the direct result of dichotomy, with prevalent dichopodial development. In the later stages of evolution with broad photosynthetic blades, distal intercommunication became common, linking the originally free veins first into a coarse and later into a finer network. These ultimate changes throw no new light upon the earlier comparisons, but they have added greatly to the efficiency of the photosynthetic blade.

We thus conclude from the details of its specialised state that the fern leaf is of cladode origin, as witnessed by the morphology of its conducting system. For the meristeles and their derivatives may all be traced either ontogenetically or by comparison to simple stelar sources, comparable with those of other vascular organisms (Rhyniaceae) which, though themselves dichotomous, did not bear organs that attained the rank of cladode leaves. This does not, however, account for all appendages. Though the microphyllous leaves of certain early Archegoniatae were without vascular supply, others in a higher state of development are approached by strands emanating from the central stele, which in certain cases advanced into the microphyll itself. The point of insertion of these microphyll-traces, whether in *Asteroxylon* (Fig. 82), or in *Lycopodium* and *Selaginella*, appears to be without any exact or constant relation to the flanges of xylem present where the stele is large. In fact, the same principle applies for them as for the insertion of the pinna-traces in Ferns (Chapter XVII, p. 348).

ROOTS

The vascular tissue in the root of the Archegoniatae remains to be considered. A monarch stele appears in the Stigmarian rootlets, and in those of

¹ Davie, *Trans. R.S. Edin.*, 1914, p. 349, and 1917, p. 1.

Isoetes, as well as in the smaller rootlets of *Lycopodium* and of *Selaginella*; even in the Ophioglossaceae monarch roots are to be found, which dichotomise like those beforenamed. In all of these the xylem is represented by a purely tracheidal tract, and the details accord with that of the simple stele of the smaller stems of the Psilophytales, excepting that the protoxylem is defined and exarch, and the tracheides more fully developed (Fig. 291 *bis*).

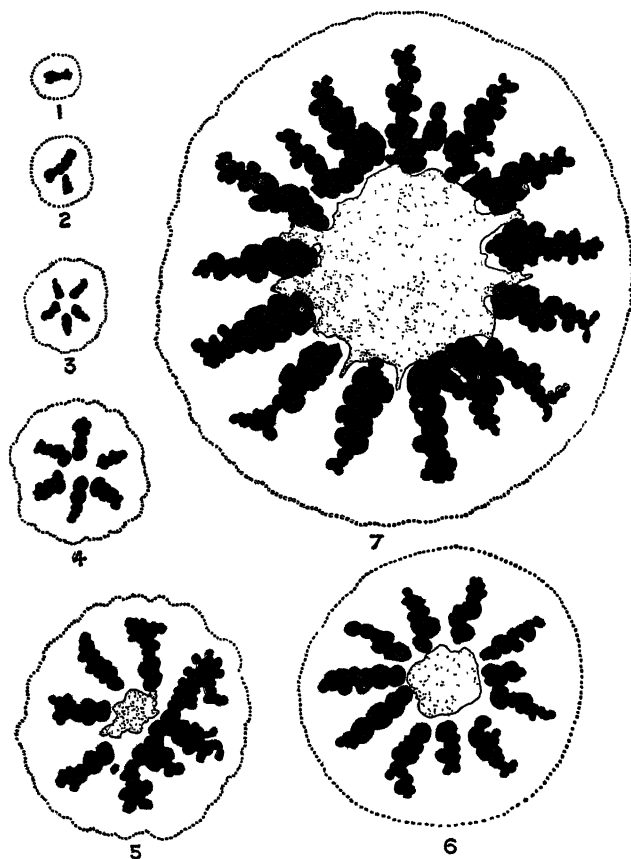


FIG. 438.

Danaea nodosa. Series of sections, all drawn to the same scale, showing the changes in complexity of the xylem which accompany increase in size. 1 and 2 from sporeling plants; 3 and 4 from young plants; 5 and 6, medium-sized roots from adult plants; 7, stele of a very large root. In 5-7 the pith is sclerosed. $\times 50$. (After Wardlaw.)

Monarch structure has also been seen in the sporeling roots of *Danaea*; from this simple state onwards the roots of *Danaea* are successively larger and show progressive structure in relation to their size, as is seen in Fig. 438. The sections are here drawn to scale, and the usual increase in number of xylem rays seen successively in those of larger size is entered in the third

column, while the ratio of their number to the diameter of the stele remains approximately constant, as the adjoining table shows :

ROOTS OF *Danæa nodosa*

Based on Fig. 438

No. of Section.	Diameter in mm.	Number of Rays.	Ratio.
1	·136	2	·068
2	·182	3	·060
4	·373	6	·062
6	·755	11	·068
7	1·317	16	·081

The reason for quoting these facts here is for comparison with similar results derived from the drawings of C. Bertrand of sections of the underground rhizomes of *Psilotum*, where also a radial structure appears : and the ratios of number of flanges to size, as represented by Bertrand, again remain approximately constant, as the table based upon them shows :

RHIZOMES OF *Psilotum* (BERTRAND) ¹

Number of Figure.	Diameter of Stele as Figured in mm.	Rays.	Ratio of Diameter to Number of Rays.
130	20	2	10·0
151	32	3	10·3
175	40	4	10·0
161	60	5	12·0
162	70	7	10·0

Naturally this similarity in radial structure and in reaction to size does not prove morphological identity of a Psilotaceous rhizome with a Fern root. But it greatly strengthens the presumption that both parts are essentially alike in nature. This conclusion is believed to apply for vascular Archegoniates as a whole. It seems probable on general grounds—and the anatomical evidence is in accord—that the origin of roots has been by specialised development of underground rhizomes. The simplest in structure resemble the simplest stalks of the undifferentiated Psilophytaceous fossils, while the greater complexity of the largest follows lines similar on the one hand to the rhizomes of the living Psilotaceae, and on the other to the aerial stems of primitive vascular plants, such as the Lycopods and the Coenopterid Ferns.

¹ This table is based on Figs. 130-162, from Bertrand, *Arch. Bot. du Nord*, Lille, 1881.

CAMBIAL THICKENING

The chief place in this description of the conducting tracts of Archegoniate Plants has naturally been given to those of primary origin. We have passed in review those structural complications adopted by the larger Pteridophytes as their size increases, which have the effect of maintaining functional efficiency while depending upon primary tissues only. Those modifications become increasingly unworkable as the size increases : indeed they raise new functional problems of their own. There is, moreover, nothing automatic about this levelling up in the proportion of surface to bulk, nor has any plant possessing only primary development attained the greatest success as measured by size. Even Tree Ferns and Palms have failed with their primary construction to compete with the Gymnosperms and Dicotyledons, in which secondary cambial growth is the rule.¹ Nevertheless, every Class of the Pteridophyta has at one time or another developed cambial activity in some degree ; but in none of those now living is it a dominating feature, as it is in certain Seed-Plants.

The factors which more than any others have made cambial thickening a success are, first, the unlimited capacity for forming new masses of tissue, to balance the increasing demands for strength and transit in a shoot-system built upon an unlimited scheme ; and, secondly, the fact that the masses of secondary tissue are as a rule vitalised, partly by the medullary rays of living tissue that penetrate the secondary zone, partly by the presence of living cells intermixed with the tracheal elements of the wood, and forming with the rays a connected system that permeates the whole. Such advantages resulting from cambial thickening make it appear strange that so many Pteridophytes have tried it, and developed it with some degree of success in early fossil types ; while their living representatives depend largely or entirely upon primary tissues for their stability, and for the transit of materials.

In *Psilotum* and *Tmesipteris* feeble traces of a secondary formation of wood have been recorded ; but there is no definite cambium, though there is a radial arrangement of the tracheids. Whether or not this be held as the result of a true cambial activity the secondary structure fades out upwards. Among the Articulatae, however, in the Sphenophyllales there is a definite band of secondary wood of cambial origin, surrounding the primary core ; but they have left no modern representatives (Chapter IX). In the Equisetales a broad zone of cambial wood adjoins the attenuated relics of the primary wood within, and it develops in sufficient volume for plants of dendroid habit. These have, however, left behind as their present-day representatives only the herbaceous genus *Equisetum*, with its primary system corresponding closely to that of *Calamites*. It was thought at one time that the woody masses at the nodes of the living Horsetails represented a relic of secondary activity,

¹ *Size and Form*, 1930, chaps. ix., xi.

such as that seen in the fossils ; but a closer examination has shown that this is not so, and the exiguous wood is wholly primary (Chapter X, p. 178). The cambial thickening in *Lepidodendron* and *Sigillaria*, described in Chapter XII, supplied the giant Lycopods of Palaeozoic time, and it is faintly featured in the stock of *Isoetes*. Nevertheless, all secondary conducting tissue is absent from the other modern representatives of the Class. Lastly, secondary thickening had a somewhat tentative hold on the early Filicales. It is seen sporadically among the Zygopterids, in *Metaclepsydropsis*, and in *Ankyropteris* ; but the best known instance is in *Botrychioxylon*, which is perhaps identical with *Zygopteris primaria*. Though such cambial increase seems never to have taken firm hold in the Filicales it is seen still to survive as a feeble development in the modern *Botrychium*, with a correlative reduction of the primary wood (Chapter XVII, p. 331).

Though the Rhyniaceae do not themselves possess cambial increase there is a growing body of observation which shows that among the relatively large fossils of the Devonian Period secondary increase of the conducting tracts did take place. As examples of this may be specially mentioned *Schizopodium*¹ and *Aneurophyton*.² As compared with typical cambial thickening on the one hand, and primary wood on the other, the added masses of wood in such plants seem to take a middle place. Though the tracheids are often disposed in radial rows there appears to be no cambium as such. Their state seems to be like that of the nodal xylem of *Equisetum*. This is not the place to discuss these matters fully ; but such facts suggest that among the earliest vascular plants where the size is great, vascular increase was a widespread fact, and that the additions like those of the normal cambial wood were disposed around the tracts of primary wood, whether these were coherent and cylindrical in form, or fluted, or even disintegrated. In this they afford material for comparison with the anomalous thickenings later seen in the Pteridosperms. The fact that is of the greatest interest to us here is that these secondary growths, whether truly cambial or not, faded out in the Mesozoic Period, and they are only represented as vestigial features in the modern Archegoniatae. It must remain an open question why that was so. It is not sufficient to say that the present Archegoniate Flora consists of relatively small plants ; for the larger Marattiaceae and Tree Ferns compare in size with many of the larger fossils, and they present a most complex primary structure. The plain fact appears to be that the Archegoniatae of the present day, for some obscure reason, have advanced their primary construction, and relinquished their heritage of cambial development.

¹ Harris, *Phil. Trans.*, vol. 217, p. 395, 1928.

² Kräusel and Weyland, *Beitr. z. Kennn. d. Devonflora*, iii., 1929.

The general position arrived at by comparison of the vascular system in stem, leaf, and root in the Pteridophytes is that these several parts are all the result of differentiation according to function from a single structural type. It may be visualised as a spindle-shaped body traversed by a simple conducting tract. It will have assumed early a power of branching, in the first instance by dichotomy. It would have been open to photosynthetic development of its superficial tissues above ground; while the basal region was absorptive, and became specialised as ultimately of root-nature. On the other hand a distal region was retained throughout its evolution for spore-production. The anatomical evidence, as summarised in this Chapter, is compatible with the origin of the several vegetative parts designated stem, leaf, and root, from this simple source, and their conducting tracts are seen to have followed the characteristic development of each.

In the Pteridophyta we see a climax of primary development of the conducting system, in organisms enlarging conically upwards, but habitually lacking the aid of cambial thickening. The result has been an increasing elaboration of the stelar tracts delimited as a rule by endodermis from the surrounding tissues. Though that elaboration is frequently related to the external form of the parts in question, nevertheless it is in great measure independent of the external contours. That there is an intimate size-relation has been shown by numerous tables of measurement detailed in *Size and Form*¹. The results may also be independent of unity by descent. This is testified by the presence of Solenostely on the one hand in living species of *Selaginella*, and on the other in the Filicales. Some morphoplastic factor appears to influence enlarging organisms independently of one another. In fact, stelar modelling is homoplastic. If that be so, then clearly the results cannot be used as indications of affinity, except in circles of close relationship. Thus stelar morphology takes a place for comparative purposes comparable to that of cambial thickening; these are features which have often played complementary parts in evolution. But inasmuch as the former has priority in its incidence, whether in the individual or in the race, it will take precedence over secondary changes.

¹ Bower, Macmillan & Co., 1930.

CHAPTER XXIX

SPORE-BEARING MEMBERS

A. BRYOPHYTES

THE Archegoniatae form a rough series in respect of the complexity of their Spore-producing Members. It extends from that isolated capsule of the Bryophytes, which is the single result of an act of syngamy, to the indefinite number of capsules produced by the individual sporophyte of a large Fern. The relation of either of these to the nutritional vegetative region is the subject of this Chapter: it involves a general comparison of the spore-capsule, which is the normal end-product of the sporophyte in these primitive plants of the land, as regards its position, relations, and structure. In the first blush of the theory of interpolation the simplest known types of sporophyte were assumed to be the most primitive: the earlier the event of spore-formation in the individual the nearer would seem to be the demonstration of its truth, and as evidence of this reference was made to the rudimentary post-sexual stages in certain Green Algae. Hence the prominence which was given in comparison to the sporogonium of *Riccia* (Fig. 23). On the basis of the arguments of Von Goebel, which have been summarised in Chapters I-V, it seems no longer possible to uphold this assumption; but rather to see in the simple sporogonia of *Riccia*, and of certain other Bryophytes, the results of progressive reduction, by which an intervening photosynthetic stage, present in certain types now believed to be primitive, has been eliminated. Such comparisons as have been summarised in Chapter VI point rather to the Anthocerotales, in reflecting a relatively primitive state of the Archegoniate sporophyte. The problem is not so simple as was at first assumed. It seems probable that a general-purposes state, without sharp segregation of the vegetative and propagative regions, preceded that now seen in most Bryophytes. Such a type of construction of the sporogonium appears in *Anthoceros*, and is reflected less perfectly in those of many Mosses. The comparative study of their sporophyte will then start from a general-purposes body of spindle-like form, in which self-nutrition and spore-production were both effective, and not strictly localised apart from one another.

The Bryophyta have made the best of a spindle-like scheme, as presented by the sporogonium of the Anthocerotales. An early change will have been by segregation of those functions, through differentiation of a

distal capsule from a vegetative stalk of intercalary origin, with a specialised suctorial base (Figs. 6, 7). The Mosses and Liverworts will have diverged along distinct lines; in the Marchantiales (Chapter II) and Jungermanniales (Chapter III) photosynthesis has been eliminated; even the seta is colourless, while the capsule, here more strictly defined than it is in the Anthocerotales, has progressed along lines which retained a solid fertile core with its domed apex, as seen in the simplest Anthocerotales (*Notothylas*). Its cells have been differentiated as spore-mother-cells and elaters, with a varied tendency to decentralisation, as shown in the elaterophores of *Pellia* and *Aneura* (Figs. 37, 38). On rupture of the capsular wall, usually by radiating cleavages only a step more elaborated than the two that exist in *Anthoceros*, the elaters are effective in spore-distribution.

The Musci present a higher differentiation, but still the sporogonium is referable in origin to the type above sketched. The families of the Sphagnales and Andreaeales take a position intermediate in various features between the Liverworts and the Bryales, but particularly in respect of their sporogonia (Chapter IV). That of *Sphagnum* has no continued apical growth, while the endothecium forms the columella, and the dome-shaped archesporium springs from the amphithecium, as in *Anthoceros*. Moreover, vestigial stomata are present on its surface, suggesting that there had been a more developed photosynthetic system in the ancestry than that now seen. On the other hand, the amphithecial origin of the fertile cells presents a high state of decentralisation. In *Andreaea*, as in the Bryales, there is a continued apical segmentation, while the archesporium is of endothecial origin (Figs. 44, 46); but it still forms, as in *Anthoceros* and in *Sphagnum*, a complete dome, while the fission is by four crossed slits, as in most of the Anacrogynous Liverworts; but there is still a coherent tip in *Andreaea*. The interest lies in the variety of these comparisons, and their effect is to draw together the two Classes of the Bryophytes, relating them to a common type of construction, where nutrition and propagation were not fully segregated, while the fertile tract was central.

In the Bryales (Chapters V, VI), the structure of the capsule reaches its climax, though it may still be related by comparison to the central type above sketched. It retains its photosynthetic activities, particularly in the Splachnaceae and Buxbaumieae; but they are habitually centralised in a zone at the base of the capsule. The distal end is specialised for spore-distribution, usually with a circumscribed operculum, which covers the highly elaborated peristome. The existence of a basal photosynthetic region and a distal mechanism of distribution has a special interest in the interpretation of the barrel-shaped archesporium. This form of the archesporium may be recognised as a residuum left after progressive steps of sterilisation from a solid central dome-shaped endothecium. First decentralisation would define the columella, surrounded by the archesporial cylinder. This shows

signs of having been truncated below, by sterilisation correlative with the formation of the enlarged apophysis, and above by sterilisation correlative with the development of the peristome. The result is then the barrel-shaped fertile tract. Thus it appears that, even in the most advanced types, the Moss-capsule is referable to a type of construction such as has been sketched above, but specialised along lines of high spore-output, and of an effective spore-distributing mechanism. Meanwhile a certain power of photosynthetic nourishment was retained, and even at times specially developed by a sort of evolutionary throw-back, as in *Splachnum* (Fig. 64). The form of the simple radial spindle is retained throughout, though subject to detailed modification.

This brief re-statement of the developmental facts and inferences will have brought into prominence the limited character of the Bryophyte sporogonium. Its inherent disabilities are: (i) its physiological dependence, and limited duration; (ii) the feebleness or entire absence of its apical growth and photosynthetic equipment; (iii) its integral archesporium; and (iv) the absence of branching. It was thus foredoomed to a cramped existence, and to relatively small size. What would be required for further advance is: (i) full physiological independence; (ii) continued apical growth; (iii) a plurality of spore-sacs giving the opportunity for succession in time of maturing; (iv) some method of amplification by branching of the capsule; and (v) an efficient conducting system. These features are all present in Vascular Plants, and they account in great measure for the dominance of the Pteridophyta, and of the Seed-Plants. To those working on such problems towards the end of the last century two alternatives appeared to present themselves, as accounting for the origin of the polysporangiate state seen in vascular plants, when expressed in terms of a body of the nature of a Bryophyte capsule: viz., septation or branching. The latter now appears as the more probable, and certainly the prevalent alternative.

In 1894 a theory of the strobilus was suggested in which the former alternative was adopted. A detailed study of the Morphology of Spore-producing Members had brought into prominence the fact that septation of sporangia does occur, both in the Pteridophytes and in Angiosperms.¹ The effect of this was to suggest a *theory of septation* of a sporogonial capsule, such as that of *Anthoceros*, subdividing the concrete archesporium into a number of fertile patches, each of which would develop into a substantive sporangium; and that thus a polysporangiate state would result. The numerous instances of synangia in early Pteridophytes appeared to support this view, which formed the foundation for a "Theory of the Strobilus."² According to it a strobilus, such as that of *Lycopodium*, would be the correlative of a single sporogonial capsule. This theory was further developed in the *Land Flora* of 1908, chap. xi.,

¹ Bower, *Phil. Trans.*, 1894-1897.

² *Annals of Botany*, vol. viii., 1894, p. 343.

and appended to it was the hypothesis of the *enation of microphyllous sporophylls*. In view of the Palaeozoic evidence now available septation is no longer probable as a primary source of origin of the numerous sporangia in Microphyllous Pteridophytes, and a strobilus can no longer be held as the correlative of a single sporogonial capsule. Nevertheless, the facts of septation still remain to show how in the Marattiaceae and Ophioglossaceae, and in the stamens of certain Flowering Plants, the number of sporangia may thereby be increased.¹ *On the other hand, enation is still retained as a probable mode of origin of microphylls.*

B. DEVONIAN FOSSILS

Till the second decade of this century the gap between the Bryophytes and Vascular plants had remained unbridged, except by hypotheses such as those above stated. Nevertheless, few doubted that some real relation existed between plants so alike both in life-history and in habitat. But there still appeared no observational link, beyond the early records of Dawson on *Psilophyton*. The discovery of the Devonian fossils of Röragen, Rhynie, and Elberfeldt, and lastly those of the Walhalla Series of Australia, also from early Devonian strata, have provided important clues of positive fact drawn from the earliest known Land Flora. Here it is not the plants as a whole but their sporangia that claim special attention: the immediate question is the relation of the capsular unit of the Bryophytes to the plurisporangiate state of living Pteridophytes, as now illuminated by these Devonian and other fossils. *Sporogonites* first described from the Lower Devonian of Röragen by Halle, and later by Lang and Cookson from Australia, supplies evidence of an early existence of a sporogonium-type of structure, containing a dome-shaped spore-sac curving over a central sterile columella, and covered in by a thick capsular wall, after the manner of *Sphagnum*, or of the young state of *Anthoceros* (Fig. 439). But it was without any clearly defined opening mechanism.² There is no definite proof whether these capsules were solitary, or borne on a branch-system; nor whether the stalk was or was not vascular; but the demonstration of such a body has its positive value when taken in relation to other recent discoveries. For in the Rhynie fossils also the sporangia are distal, with a thick capsular wall, and with the dome-shaped spore-sac sometimes surrounding a sterile columella; but they were borne on forked vascular stalks (Chapter VII, Figs. 78, 79). The inference from these facts that the sporogonial head of a Bryophyte finds its counterpart in the distal sporangium of the Psilophytales cannot be held as proved. This step must be awaited till further data are available for *Sporogonites* or similar fossils, particularly as to the structure of the stalk and basal region. But the

¹ Bower, *Morphology of Spore-producing Members*, ii., Dulau, 1896.

² Halle, Stockholm, 1916. Lang and Cookson, *Phil. Trans.*, B., 1930, p. 150. The above details are based on Halle's specimens.

probability of its truth seems sufficiently strong to justify acceptance as a basis for a working hypothesis.

The similarity between the diffusely forked fertile stalks of *Hornea* and *Rhynia* (Figs. 78, 79), many of them bearing solitary distal sporangia, and the diffuse "sporophylls" of *Stauropteris* from the Lower Carboniferous, has often been remarked. These fossils, together with *Sporogonites* itself, and some others, suggest an early type of vegetation having in common solitary, distal sporangia, borne on dichotomising terete stalks, homosporous and eusporangiate, and without elaborate opening mechanisms. The prevalence of such a generalised type in early Palaeozoic time, in a flora where there appears to have been little choice of types, is an important fact in comparative morphology. The sporangia were borne on a photosynthetic sporophyte without flattened blades, though already demonstrated as vascular in certain cases. From a structural point of view these primitive plants compare with some of the most generalised types of the Bryophytes; but they fill in certain of the deficiencies above noted in these, for they possessed physiological independence and vascular organisation, as well as apical growth and branching. Thus endowed, though still rudimentary in many respects, being rootless and without any expanded leaf-surfaces, these plants attained complexity and size beyond that of any living Bryophytes. Nevertheless, they still possessed the distal spore-capsule as a fundamental though not always constant unit. Here it may fitly be noted that branching has been recorded as an occasional abnormality in living Bryophytes. Certain rare examples are shown in Fig. 440, and instances have also been seen among Liverworts.¹ It is not suggested that such happenings have any direct relation to what is seen in the early fossils. They are quoted here to show that branching of a sporogonium is not a fact outside the frame of current observation.



FIG. 439.
Sporogonites chapmani, Lang and Cookson. Upper portion of the stalk, with terminal, capsule-like structure. $\times 54$. (*Phil. Trans.*, B., vol. 218 Pl. II., Fig. 11.)

¹ Pfeffer, *Jahresbericht Naturf. Gesellsch. Graubundens*, 1868, Heft xiii. Leitgeb, Graz, 1876, "Ueber verzweigte Moos-sporogonien." Also Leitgeb, *Rab. Krypt. Flora*, iv., Abth. i., p. 39.

It has been seen in Chapter VII how the same type of construction as that of *Rhynia* and *Hornea* underlies the more complex plant of *Asteroxylon* (Fig. 79). Its larger size carries with it the added feature of numerous leaves of the microphyllous type, borne upon the larger axes; but these are absent from the basal regions, and are not associated with the distal *Hostimella* twigs which bear the sporangia. The relatively simple, generalised type of Vascular Plant seen in *Hornea* and *Rhynia*, and the more elaborated state of it in *Asteroxylon* and some others, may serve comparatively as indicating possible lines of specialisation which might lead onwards to the megaphyllous and the microphyllous Pteridophytes.

In the diffuse type of the Devonian fossils the sporangia, though increased in numbers by dichotomy of the shoot, still behaved each as a unit, distal and

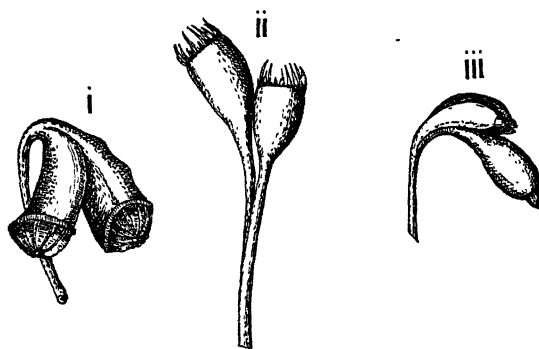


FIG. 440.

Branched Moss-sporogonia. i.=Dicarpy of *Bryum versicolor*, after Pfeffer. ii.=Dicarpy of *Hypnum incurvatum*, after Leitgeb. iii.=Tricarpy of *Bryum pallens*, after Pfeffer.

as a rule isolated. But all higher types of vascular vegetation have tended more or less clearly towards the *association* of such units; this is, indeed, the simplest of those features that mark their morphological advance. The biological advantages of communal nourishment from a central source, and of mutual protection, naturally follow from it; moreover, the plant, or the single branch, no longer depends upon the welfare of one unit, but of many. Such a conception of the association of units involves an upward outlook on the evolution of the spore-producing parts. The chief factors that lead to this association of sporangia are: (i) an abbreviation of the stalks, so that a whole branch-system is condensed into a more or less compact form; (ii) fission partial or complete of the individual cyst may be a feature; and (iii) interpolation of sporangia between, or other additions to those already existent, may also find a place. At times such changes as these appear as though imperfectly carried out; and the result may then be anomalous states that are difficult of resolution in terms of the normal. These add reality to the general conception of the upward trend. In illustration, the well-known

two-lobed sporangium of *Hornea Lignieri* presents a state that may be interpreted either as an imperfect forking or as a result of fusion of sporangia, according as an upward or a downward aspect of such a fact is entertained. Here the former is adopted (Fig. 441). On the other hand interpolation, such as is seen in the "mixed" sori of Ferns, may be held to be either a result of imperfect synchronisation of sporangial formation, or as an actual addition of new primordia between those formed earlier (Figs. 307-313). Here the latter interpretation would appear to be true.



Fig. 441.

Hornea Lignieri. Two well-preserved sporangia, Sm^2 and Sm^1 , cut in accurate longitudinal section, terminating two slender stems. The lower sporangium is bifurcate, the upper simple. Note the columella in each, overarched by the spore-bearing layer. $\times 12$. (After Kidston and Lang.)

The several Classes of the Pteridophyta have been treated in detail in Chapters VII to XXII, and in each the lines of specialisation have been traced, both as regards the antecedent vegetative system which is ancillary to the final end, and in relation to the spore-producing members by which that end is attained. Here the latter will be passed in review for the several Classes of the Pteridophytes from the aspect of upgrade development : there is no intention, however, of overlooking the possibility of downward simplification. In adopting this general view there must be complete freedom from preconceptions based on the morphology of Seed-Plants ; at the same time full allowance must be made for homoplasy in the several phyla, under the influence of external conditions that will have been essentially similar for them all.

C. MICROPHYLLOUS PTERIDOPHYTES

The Psilophytales as described in Chapter VII now form a starting point for an interpretation of the living Psilotales, which, as suggested in Chapter VIII, may be looked upon as organographic experiments caught early on the evolutionary upgrade, and left still living but in a primitive state. This applies particularly to their spore-producing parts, which have always presented difficulties of interpretation in terms of plants higher in the scale. But if examined as part of an up-grade *nexus*, including also the Anthocerotales and Psilophytales, even the fertile twig ("sporangienstand") becomes intelligible. The older interpretations have already been discussed (p. 144); of these only that of Miss Sykes need be recalled,¹ for her interpretation accords with the upward view here adopted, and it will readily account for the frequent abnormalities seen in both genera (Fig. 86). The fertile twig is held to be a group of organs, consisting normally of an axis, usually two "*Thursophyton*" leaves or microphylls, and a distal synangium. Compared with *Asteroxylon* the axis is of the nature of a "*Hostimella*" branch, but invaded by "*Thursophyton*" leaves, which are definitely associated with the normal synangium: the latter represents a highly condensed and abbreviated *Hostimella* branchlet. The whole fertile shoot which bears these twigs in *Psilotum* (Fig. 87), or in *Tmesipteris* (Fig. 84), would be of the "*Thursophyton*" type, as seen in *Asteroxylon*; this from time to time gives rise to fertile twigs with each of which two microphylls are associated. In abnormal instances, whether of *Psilotum* or of *Tmesipteris*, a single distal sporangium may replace the synangium; or the fission may be incomplete (Fig. 86). In these intermediate states a parallel may be found with the two-lobed sporangium of *Hornea* (Fig. 441). On the other hand, the fertile twig or "sporangienstand" may be elongated, and a succession of synangia with a single distal sporangium may be produced. These on the present hypothesis would represent irregular instances of branch-systems not fully condensed down to the type that has become normal.²

The most notable innovation seen in the Psilotales as compared with *Asteroxylon* is the invasion of the fertile or "*Hostimella*" region by microphylls; that is, according to the interpretation here given. These together with the synangia constitute in its simplest form the *composite cone or strobilus*, a body which will be seen to figure in other microphyllous types on a much larger scale. Further, the synangia present a simple state of association of sporangia which has obvious advantages in mutual protection and nutrition, provided the mechanism of dehiscence be not highly specialised. This state may have resulted either from actual fusion, or from fission im-

¹ *Ann. of Bot.*, xxii., p. 86.

² See Miss Sykes' figures, *Ann. of Bot.*, xxii., p. 525.

perfectly carried out. Synangia are not uncommon in early Pteridophytes, and wherever they occur the same uncertainty as to origin may be expected to arise.

The very ancient phylum of the Equisetales may be considered next, as one of a succession of types which appear to illustrate stages in a similar invasion of a fertile *Hostimella* branch-system by microphylls. The essential features have been described and compared in Chapter X. The sporangio-phore of the Class is of the type seen in *Equisetum* (Fig. 120), but the number of sporangia borne on each is variable: in *Equisetum* the number is relatively large, in *Calamostachys* it is usually four, but in *Calamostachys paleacea* there is only a single sporangium, though this is not erect nor distal, but inverted as in other Equisetales.¹ The conclusion of Lady Isabel Browne, from wide comparison of Equisetales, ancient and modern, is that the balance of evidence is in favour of the primitiveness of the mono-sporangiate or bi-sporangiate types of sporangiophore.² In *Archaeocalamites*, from the oldest Carboniferous strata, the cone consists of an axis bearing superposed whorls of sporangiophores without bracts: in fact the condition is much the same as that of the modern *Equisetum* (Fig. 127). It may, however, be interrupted by scattered whorls of bracts at long intervals; thus offering a comparison with *Phyllothea* (Fig. 122), or with the state seen as an occasional abnormality in *Equisetum* (Fig. 121). Such instances show that, whether in the ancient fossils or in living Horsetails, there is no obligatory relation between sporangiophores and bracts. Nor is that relation, so far as it exists, exact even in favourable cases. The main facts have already been stated in Chapter X; and they may be amplified by reference to the careful summary of the details up to 1927 by Lady Isabel Browne.³ These lead to the definite opinion that the bractless cone, as seen in *Archaeocalamites* and in *Equisetum*, was really primitive; and that eventually bract-leaves were intercalated, either at irregular intervals as in *Archaeocalamites* and *Phyllothea*, or with regularity as in *Calamostachys* and *Palaeostachya* (Figs. 128, 129). These bracts and sporangiophores have been strikingly different from one another in character from the earliest times. Moreover, neither in number nor in relative position are they conformable. In particular, in *Calamostachys* the successive sterile whorls alternate with one another, while the fertile sporangiophores are superposed, as they are in the bractless cones of *Archaeocalamites* (Fig. 127); hence the hypothetical advent of the bracts has not displaced their order. Lastly, the relative positions upon the internode are not constant: for in *Palaeostachya* the sporangiophores appear axillary (Fig. 129), in *Calamostachys* they are inserted half way up the internode (Fig. 128), while in *Cingularia* (Fig. 130) they stand immediately below the bracts. Such facts accord ill with any

¹ See Hirmer, *l.c.*, Figs. 544, 545.

² *Ann. of Bot.*, xli., 1927, p. 316.

³ *Ann. of Bot.*, xli., p. 301.

view of the homology of bracts and sporangiophores. They suggest that the cone bears two distinct types of appendage, loosely related one to another: the sporangiophore, which is the correlative of a fertile twig of a "*Hostimella*" branch-system, condensed and transformed; while the bract-scale is a microphyll, comparable with the "*Thursophyton*" scales. Further, that the state seen in *Calamites* is the result of invasion of a bractless cone by "*Thursophyton*" scales, while the annulus of *Equisetum* represents for it the limit of that advance. The biological importance of the invasion was chiefly protection where the cone is lax; but in compact cones the enlarged distal ends of the sporangiophores may often form a sufficient protection for the young sporangia till the parts separate by elongation of the axis when the spores are ripe.

A divergent view from this has been held by Von Goebel, based upon experimentally grown ("vergrünte") lateral shoots of *Equisetum Telmateja*,¹ where sporangia appear on parts that graduate into normal leaves. This sometimes occurs also in nature. The first specimen quoted by Von Goebel (I.) bears at the base normal sporangiophores, and higher up appendages of intermediate type to bracts, and finally normal scale-leaves. But specimen (II.) has no typical sporophylls. In such examples all intermediate stages may be seen between sporangiophores and foliage leaves. If no other Equisetoid strobili were known except those of the living *Equisetum* the argument based upon such intermediate stages between sporangiophores and scale-leaves might be acceptable. But against it account must be taken of Equisetoid strobili as a whole, including those of the fossil Horsetails that are without bracts, as well as those which have them; also of the great majority in which no intermediate types are seen. When this aspect of the facts is duly considered the distinctness based on the great majority of instances will appear to be the normal; the intermediates, of rare occurrence or artificially induced, will appear as abnormalities, of doubtful validity for morphological argument. Further, the high degree of stability in distinction between bract-scales and sporangia in the Lycopodiales will have its weight as a parallel instance (Chapter XI). On the other hand, the problematical state of *Sphenophyllum fertile* might be quoted in support of Von Goebel's view, if interpreted as it has been by Scott (see p. 154).

A third example of cones which may be regarded as composite in the sense above described is presented by the Sphenophyllales, which offer many points of similarity to the Equisetales. But here the sporangiophore is itself a less stabilised body: its variability depends partly on the number of the sporangia, partly on the branching of their less standardised stalks. The essential details have been given in Chapter IX. The cone is a fairly compact body, taking a position intermediate between the lax fertile shoot of the Psilotales and the more compact cone of the Equisetales. It is composed of an axis bearing successive whorls of superposed bracts, which are cup-like

¹ *Organographie*, 1930, Fig. 1314, I, II.

below owing to lateral fusion, but they have separate distal teeth. The sporangiophores vary considerably in detail : each is opposed to a subtending bract, and derives the vascular supply from it. The exact relation may, however, be obscured by the fact that the branching takes place low down, even within the cortex of the axis, while the pedicels may be adherent for varying distances upwards to the cup-like whorl of bracts. In the more complex cones, and particularly in *Cheirostrobus*, this may appear to raise difficulties (Fig. 114); but these are made more intelligible by comparison with the simpler types.

The fact that the sporangiophore in the Sphenophyllales is constantly opposite to a subtending bract has led Hirmer to the designation of the two parts collectively as constituting a sporophyll-unit ("Sporophyll-Einheit"), each consisting of an adaxial fertile and an abaxial sterile part.¹ The relation of these parts is certainly constant in the Sphenophyllales, as also is the relation of the sporangium to the subtending bract in the Lycopodiales. But the variability shown in this respect in the Equisetales would suggest that here we deal with a collocation of parts biologically advantageous, rather than with one historically and morphologically constant for plants at large, however firmly it may be established in certain Classes. For microphyllous types generally the bract and the sporangiophore are here regarded as historically independent parts. By a study of the cones from his own point of view Hirmer has resolved the complex and variable arrangements of the sporangiophores into forked branch-systems; for instance, in the special case of *S. Dawsoni* (forma α) the two-armed sporangiophore-branches lie alternately above and below the one-armed branch : a very convenient space-arrangement. Each branch bears a single pendent sporangium (Fig. 116). The adoption of Hirmer's view of a "Sporophyll-Einheit" is not essential to acceptance of his resolution in terms of fertile twigs and bracts.² The important fact is that such a resolution should follow as the result of detailed study. The Sphenophylloid fructifications may be arranged in series of progressive branching : proceeding from the single sporangium of *S. trichomalosum* (Fig. 107) to the compact rosette of *S. majus* (Fig. 111); then to the more complicated systems of *S. Roemeri* and *Dawsoni* (Fig. 116); and finally to that of *Cheirostrobus* (Figs. 113, 114). Thus arranged they appear to illustrate various degrees of complexity of branching in a lax type of sporangiophore, distantly comparable on the one hand with that of the Equisetales, on the other with the *Hostimella* branching of *Asteroxylon*, or even with that of *Stauropteris*.

There remains, however, the difficult problem of *Sphenophyllum fertile* (Fig. 112). The current interpretation of this cone has been that the bract, usually sterile in the genus, has developed as a fertile sporangiophore. But another resolution of this cone is possible in terms of the bractless cones of

¹ *Handbuch d. Palaeobotanik*, 1927, p. 355.

² *I.e.*, pp. 355-360.

the Equisetales. If in *S. fertile* the cone had been actually bractless, like that of *Equisetum*, and the first forking were anteroposterior (as Hirmer finds in his scheme for the sporangiophores of other species), then the paired sporangiophores of *S. fertile* would not represent the one a fertile bract and the other a normal sporangiophore, but two sporangiophores of common origin by anteroposterior fission. On this point Lady Isabel Browne has noted that "more or less regular superposition of traces of successive whorls (of sporangiophores) occurs commonly in cones of *E. maximum* and *limosum*, and more rarely in *E. palustre* and *arvense*."¹ There would then be no need to assume fertility of bracts that are so constantly sterile in the Class. The result of such comparisons is that the sporangiophores of the Sphenophyllales may each be resolved into modifications of branching of a *Hostimella* type; while the associated bract, where it occurs, is a result of invasion of the cone by enation-leaves. The cone would on this interpretation be composite, according to the Calamarian type: consisting of an axis bearing sporangiophores and subtending bracts. But these, however regular in their relation, do not constitute "sporophyll-units" in the sense of Hirmer; they present rather a collocation, physiologically intelligible, of parts historically distinct.

There is reason to believe that such a collocation is present also in the cones of the Lycopodiales. Each sporangium is there associated with a subtending bract which, though varying in the detail of its moulding in different genera and species, maintains its character as a simple sporophyll traversed by a median vascular strand. It is true a distal forking has been described for the leaves of the Devonian fossil, *Protolepidodendron* P. and B.; but this is quite exceptional, and it requires further elucidation.² On the other hand, very rarely two sporangia may be found in the axil of a single sporophyll³: but this is probably nothing more than an abnormality of fission. Apart from such isolated facts the sporangia and sporophylls of the Lycopodiales are remarkably constant in relative number and position in the strobilus; they and their sporophylls being arranged sometimes in whorls, but as a rule spirally. On the sterile shoot microphylls are similarly arranged, but without sporangia, though this distinction is often bridged over by imperfect sporangia holding the normal position: a fact which suggests that the sterile and fertile leaves are essentially of the same nature.⁴ Lastly, in the *Selago*-type the form of the leaf is uniform throughout (Fig. 442), though in more specialised Lycopods there may be considerable difference between sporophylls and foliage leaves (Figs. 149-151). The high degree of constancy in the composition of the cone in the Lycopods contrasts with what is seen in any other Class of the Microphyllous Pteridophytes.

¹ *Ann. of Bot.*, xxix., 1915, p. 239.

² Lang, *Trans. R.S. Edin.*, 1926, p. 791; also Hirmer, *l.c.*, p. 319.

³ *Ann. of Bot.*, xvii., p. 278.

⁴ *Ann. of Bot.*, xv., p. 255.

A detailed description of the structure and development of the sporangia of the Class has been given in Chapter XIII. Differences of form and of exact position of the individual sporangium in relation to the sporophyll have been found to exist in the several genera and species; here a brief comparative summary must suffice. For reasons there explained the *Selaginella* type is believed to be relatively primitive among living Eligulates, and *Selaginella spinulosa* among the living Ligulates. Both accord with the verbal specification given at the close of Chapter XV to help in visualising a primitive type of Lycopod. The leaves are associated each with a single sporangium inserted near to its axil, and the median planes of sporophyll and sporangium coincide; but the exact position in that plane varies. In *Lycopodium* the sporangial stalk is attached near to the base of the leaf (Figs. 181, 184, 186), and the same is seen in the sporangia of *Bothrodendron* (Fig. 199, B). In *Selaginella* it arises from the axis (Fig. 187). In certain other ligulate types it may be spread out along the leaf-surface (Figs. 164, 192, 195). In *Spencerites* it is attached distally on a narrow pedicel which bears an upturned lamina (Fig. 194). There is thus considerable variety in the point of attachment of the sporangium in relation to the axis and to the sporophyll; and the differences of relative position are of the same nature as those of the sporangiophores seen in the cones of the Articulatae. There is also considerable variety in the form and structure of these Eusporangiate

capsules within the Class. The form is essentially bivalvular throughout, with a more or less fan-like spread of the capsule right and left, while the slit of dehiscence is in a plane tangential to the axis. The stalk is slender in the types regarded as primitive (Figs. 182-3, 188-9), and oval in transverse section, with the longer axis tangential; but in *Isoetes* and *Lepidodendron* it is extended radially over a considerable area of the sporophyll (Figs. 192-4). Developmentally a like variation in radial spread (though less in degree) has been demonstrated in living species of *Lycopodium* (Figs. 184, 186). Such

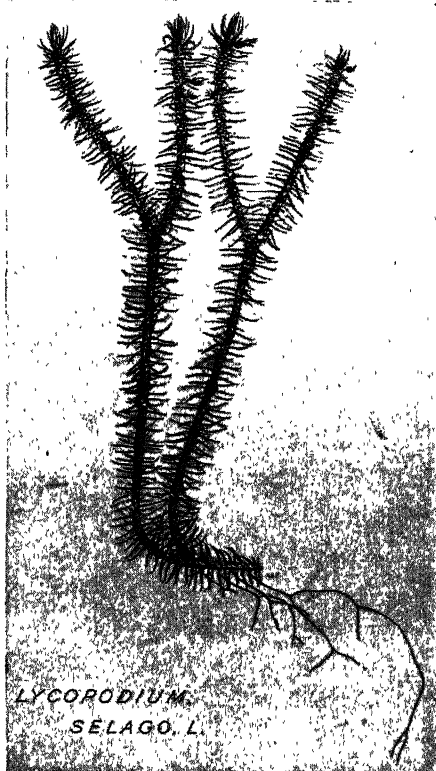


FIG. 442.

Whole plant of *Lycopodium Selago*, showing ascending and upright habit, as developed when growing protected by Heather. The equal dichotomy and the alternating sterile and fertile zones are seen, and the forking of the roots. Distally bulbils are borne. Reduced.

facts suggest a progression related to increasing spore-output. With the advent of a seed-like habit there followed other modifications, protective and structural, as in *Lepidocarpon* and *Miadesmia*: while steps towards septation appear in *Cantheliophorus*, *Isoetes*, and *Mazocarpon*. All of these, however, appear as specialised advances upon the fan-shaped capsule here regarded as primitive, and do not affect the fundamental relations of sporangium and sporophyll.



FIG. 443.
Incrustation of the strobilus of *Zosterophyllum australianum*. $\times 2$. (After Lang and Cookson.)

The bracts themselves are also subject to a specialisation which appears as progressive. In the primitive types they are like foliage leaves, being photosynthetic with plentiful chlorophyll and stomata. In *L. Selago* the margins are not extended into protective flaps, so that the sporangia are freely exposed (Fig. 183). But in those types which are regarded as advanced the sporophylls cover in the sporangia more closely (Fig. 185), while their photosynthetic power is reduced or absent, and the bracts may appear as protective chaffy scales. But the stomata are retained, and the number and position of these may vary greatly. In *L. Selago* and *S. spinulosa* the stomata are numerous on both surfaces of the scale, but in species with more highly specialised cones they may be present only on the abaxial surface, as in *L. Jussiaei*, or in *S. Wallichii* and *Lobbii*: in others they are only on the adaxial surface, as in *L. cernuum* and *annotinum*. In either case they are more numerous distally than at the base. The exact distribution of the stomata seems rather arbitrary, and requires to be worked

out in relation to the structure of the individual cones of the several types. The important point is that stomata are generally present and often numerous: and the conclusion is that they are useful as pneumathodes, seated on organs that are in close relation to the developing sporangia in which metabolism is active. Such considerations bring a biological interest to bear upon the close collocation of sporangia and bracts in Lycopods, beyond that of mere protection.

In Chapter XV the question was raised of the degree of independence of the two parts so closely related in the cones of Lycopods, viz., the sporangium and the bract. There is no room for doubt that the bract and the foliage leaf are homologous throughout the Lycopod plant (Fig. 442). The *Selago*-type shows this, and the imperfect sporangia so often found at the limits of the fertile zones demonstrate that the latter merge into the sterile

zones. Thus microphylls may exist without sporangia. The crucial question is, however, the converse : can sporangia of a Lycopodinous type exist without microphylls ? A brief abstract of Dr. Lang's results from examination of *Zosterophyllum myretonianum* and *australianum* was given at the end of Chapter XV. He found that certain of the leafless branches of this early but "thalloid" sporophyte became erect, bearing characteristic, radially arranged, stalked reniform appendages. These prove to be sporangia, which opened by a slit along the tangentially extended edge. In fact their form, function, and dehiscence coincides with sporangia of the Lycopod type (Fig. 443). Hence such sporangia may exist in this ancient Vascular Plant, but without any subtending sporophylls. Thus it is seen that foliage leaves, which are homologous with the sporophylls of *Lycopodium*, may exist without sporangia, and sporangia of Lycopodinous type may exist without sporophylls. The inference from such facts is that the Lycopodinous strobilus is also a composite structure, consisting of an axis bearing sporophylls and sporangia, but that these are parts of independent character and history.

Representative types of all the living microphyllous cones have now been examined, and their constitution considered : also certain of their fossil correlatives. In respect of each of them facts and arguments have been advanced which harmonise ill with or actually negative the view that the sporangia or sporangiophores and the sporophylls bear any constant relation to one another. Historically they certainly do not, as witnessed by the bractless cones of such ancient types as *Equisetum*, *Archaeocalamites*, and *Zosterophyllum*. In point of fact either may exist without the other. Nor does the assumption that when both are associated the sporangiophores are of foliar nature resolve the difficulty ; even though they may be held to represent a "ventral lobe" of a leaf subject to "serial fission," of which the dorsal is the sporangiophore : for the facts show that the two parts are not disposed as a whole according to any constant scheme that applies equally for both. If, however, they be organs of a nature and history distinct from one another, there will be no need to assume that they should be subject to like influences determining either distribution, number, or form. That they are actually distinct is the hypothesis which was already indicated in the *Land Flora*, and worked out later with precision and much greater available detail by Lady Isabel Browne.¹ The basal fact is that spore-production has been a constant event in every normally completed life-cycle throughout the evolution of the sporophyte. Consequently sporangia and sporangiophores take precedence over microphyllous bract-scales. *Rhynia*, *Hornea*, and *Zosterophyllum* demonstrate that precedence in leafless fossils of acknowledged antiquity. But a composite cone, with both spore-producing members and

¹ *Ann. of Bot.*, xli., p. 301.

bract-scales, is the rule in more advanced microphyllous Pteridophytes. A possible source of them both is suggested by *Asteroxylon*: the *Hostimella* twigs represent a diffuse and original type of the former, while the "*Thur-sophyton*" scales stand for the latter. If fertile twigs such as those of *Asteroxylon* were reduced and compacted into sporangiophores, or perhaps represented by single sporangia, as in the Lycopods; and if the scales were to invade the distal fertile region of the shoot that bears them, and the whole were condensed and specialised, a composite cone would result. It is suggested that this was the mode of origin of microphyllous cones. In those of them which have been analysed in earlier Chapters certain possible results of this synthesis appear actually worked out. Such differences as the living Psilotales present may be held as showing the nascent Pteridophyte in an experimental stage. We may conclude that there was not any consistent plan that imposed a standardised result for them all.

Nevertheless, some degree of relation between bract-scales and the spore-producing parts is usual. This finds its natural explanation in the advantages which follow from it. In primitive forms the function of the scales may have been chiefly nutritive, as in the *Urostachya* section of *Lycopodium* (Figs. 152, 183); but in the more specialised section of *Rhopalostachya* the scales assume an expanded form and chaffy texture, and they fit closely together like scale armour (Figs. 150, 151, 185). Here the nutritive function is in abeyance, and it is protection which they afford, together with aeration by means of their numerous stomata. Such advantages are best secured by close juxtaposition of the appendages, such as is seen in the Lycopods, Calamarians, and Sphenophylls. Doubtless an axillary relation of sporangiophore and bract-scale is the most efficient; but it is not obligatory, as appears from a comparative study of the cones of the microphyllous Pteridophytes. Hence the "sporophyll-unit" of Hirmer appears as an occasional and later, but a very natural biological accommodation, rather than a fundamental fact of organisation.

The time is hardly come to draw close comparisons between the living Pteridophyta and those early fossils known as yet only as incrustations. As material for comparison these stand in a different position from the perfectly preserved plants from the Rhynie Chert. But it is impossible to leave out of discussion some of these early fossils: for instance, *Hicklingia*, described by Kidston and Lang.¹ This plant, from the Red Sandstone of Caithness, appears as a tuft of narrow linear, branched but leafless axes, some 17 cm. in length and each about 2 mm. across, with indications of a vascular strand within. These bore solitary distal bodies of oval form, and wider than their stalks. Presumably they were sporangia, but the nature of the contents is unknown. It is a simple thalloid type of plant, with organisation comparable on the one hand with that of the Rhyniaceae, on the other with *Sporogonites*. Certain fossils from the Rhine basin illustrate (as does *Psilophyton*) the group-

¹ *Trans. R.S. Edin.*, 1923, vol. liii., p. 405.

ing of distal sporangia together. For instance, *Aneurophyton* appears to bear small tassels of sporangia on curved stalks: in *Hyenia* and *Calamophyton* somewhat similar tassels are pendent (Fig. 444, A, B, C). These all suggest simple sporangiferous branch-systems in course of condensation, from a diffuse state with isolated distal sporangia, to form associated groups showing analogy on the one hand to the microphyllous sporangiophores, and on the other to the tassel-like sori of *Botryopteris*, or *Corynepteris*. On the other hand, in *Cladoxylon* fan-like fertile appendages are found with radiating veins and deeply incised margins, while each segment terminates in a sporangium (Fig. 444, D). This arrangement suggests comparison with the sporophylls of certain Ferns in method of association of the sporangia,

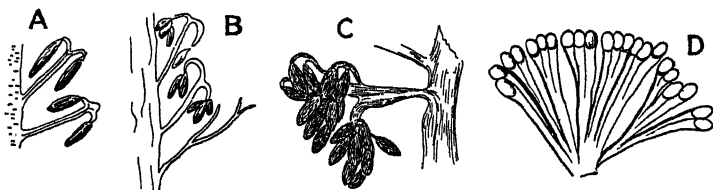


FIG. 444.

Types of sporangiophores of Devonian age, after Krausel and Weyland. A=*Calamophyton primaeum*, K. and W. Two separate sporangiophores. $\times 3.5$. B=*Hyenia elegans*, K. and W. Axes with sporangiophores. $\times 1.5$. C=*Aneurophyton germanicum*, K. and W. Sporangial trusses with the sporangia partly embedded in the matrix. $\times 3.5$. D=*Cladoxylon scoparium*, K. and W. Isolated "sporophyll." $\times \text{circ. } 2.5$.

where the ultimate branching has been in a single plane; with the result that the sporangia form a marginal row. Hirmer (*l.c.*, p. 690) remarks of *Cladoxylon* that as regards morphological construction it is obviously an intermediate form between microphyllous and megaphyllous types. Perhaps it will be better to say that it corresponds to neither of them: there is no need to commit oneself to any definite phylogenetic aspect of the comparison. Such data as these fossils show are suggestive of methods of association of sporangia; and in this position they may be left for the present. In them we probably see reflected a past period, when the sporophyte was originating those morphological patterns which in later ages have been developed with increasing precision. Their general effect in the present discussion will be to make more real the probability of an evolutionary relation between Bryophytes and Pteridophytes; for the isolated distal sporangia of *Sporogonites*, *Rhynia* and *Hyenia* point clearly towards the Bryophytes, while the association of the sporangia in *Aneurophyton*, *Calamophyton* and *Cladoxylon* is of a Pteridophytic character.

D. MEGAPHYLLOUS PTERIDOPHYTES

Turning now to the megaphyllous Pteridophytes, where each cladode leaf bears numerous sporangia commonly grouped together, and in primitive types freely exposed, it has been seen by comparison of certain early fossils that the leaves are referable in origin to dichotomous branching, and that each shank may bear a distal sporangium, as in *Stauropteris* (Fig. 294).

The branch-system on which these arise is of radial construction, as it is in the Psilophytales and many of the Zygopterids: a state which may be held as primitive. But in all the more advanced Ferns the leaf is dorsiventrally developed in relation to the axis which bears it: in which case the branching has tended towards a single plane, and this may lead to webbing and the formation of a flattened blade. If each sector of such a blade bears a distal sporangium its position will appear marginal, a state that is actually seen in *Cladoxylon* (Fig. 444, D). A like marginal position of the individual sporangium is retained in the Ophioglossaceae and Schizaeaceae (Figs. 279, 293, and 305). In this feature these archaic types of Fern appear as possessing, though in modified form, the original traits of the sporangium, viz., its unit character, and its distal (or marginal) position. When Prantl in 1881 designated a single marginal sporangium of the Schizaeaceae a "*monangial sorus*" he anticipated by half a century a position which has now found its support in fossils then unknown. It is only in the latter half of that period that the acceptance of his view has been fully justified by the observation of distal sporangia in the Psilophytales, isolated on forked vascular stalks. In the same Memoirs on the Hymenophyllaceae and Schizaeaceae as led him to the recognition of this feature he also worked out the dichopodial development of the Filicineous frond, now styled the megaphyllous or cladode leaf. This has been dealt with in Chapter XVI. On a basis of purely comparative argument Prantl was thus a pioneer of modern Archegoniate Morphology.

In many of the primitive types of Ferns which have adopted dorsiventrality of the cladode leaf a marginal position was retained either for the individual sporangia, or for soral groups of them. These are habitually seated upon the vein-endings, which may be taken as representing the terminals of the constituent branches of the cladode (Fig. 294). But often the sporangia are found *associated in groups* around a vein-ending: such a group is a *primitive sorus* (Fig. 295). Advantages of communal supply and mutual protection were thus secured. The sporangia themselves tended to become dorsiventral in relation to the central receptacle, and thus came into existence the *radiate-uniseriate type of sorus* in which all the sporangia are approximately of equal age. First came the tassel of distinct pear-shaped sporangia (which may well have resulted from a condensation of a branch-system), as seen in the Botryopterids and Zygopterids. It is a minor step from this to their closer association seen in *Corynepteris* (Fig. 296), with finally a fusion of the sporangia to form a solid synangium. Such changes of construction often accompanied a transition of the sorus from the margin to the surface of a flattened blade, as in *Ptychocarpus* (Fig. 301). But not necessarily so: for in the Ophioglossaceae the marginal position was strictly maintained. A relatively primitive state appears in *Botrychium* (Fig. 229, C-E); possibly *Helminthostachys*, with its multitudinous marginal spor-

angiosperms, presents a more primitive type still (Fig. 299, *F, G*). Ferns that show such features as these belong to the *Simplices*, and are regarded as primitive megaphyllous types.

There is an essential difference in the method of elaboration of the spore-producing organs between the microphyllous and the megaphyllous Pteridophytes. In the first instance both appear to have proceeded from a branched thalloid shoot with isolated distal sporangia of relatively large size : in both an early step has been the association of a plurality of sporangia upon a common receptacle, with vascular supply ; apparently this has been by condensation from a diffuse branch-system. *In the microphylls we call the result a SPORANGIOPHORE, in the megaphylls a SORUS* ; but both have probably originated along similar lines. Here the parallel seems to stop. In the microphylls the further elaboration is by increase of numbers of the sporangiophores, and by the association of these (or of isolated sporangia), into strobili, rather than by elaboration of the sporangiophore. In some instances there may be enlargement of the single sporangia, as in *Cheirostrobos*, or in the Lepidodendroid Lycopods ; or tentative steps may have been taken towards a seed-habit. Excepting such changes the Microphyllous Pteridophytes have not elaborated their immediate spore-bearing parts beyond the condition of a receptacle bearing a small number of relatively large sporangia, or a single one. In the Megaphyllous Ferns this state is matched by the radiate-uniseriate sorus of the *Simplices*, with its central receptacle, bearing a limited number of eusporangiate sporangia, seldom of very large size. But this state, as seen in relatively primitive Ferns, is only the starting point for further developments of high organographic interest. These involve extensions of the receptacle that are very various in detail, accompanied by an increase in number, but with a progressive decrease in size of the sporangia, and in the spore-output from each : at the same time the mechanism for the ejection of the spores becomes highly specialised. The details of such developments have been described in Chapters XVIII-XX ; here it will suffice to point out briefly the salient features of these advances.

The rosette-like sorus of the *Simplices* may be extended either along the margin or the surface of the part that bears it, with fusion and often fission of the sporangia. This is seen respectively in the Ophioglossaceae (Fig. 299), and the Marattiaceae (Fig. 302, *A, B, C, E*), while in *Christensenia* the widely expanded and reticulate blade bears many superficial rosette-like sori showing evidence of their origin by fission of the receptacle (Fig. 302, *D*). All these are variants on a primitive type of sorus with low receptacle, on which the sporangia originate simultaneously and are often fused together. Provided the receptacle itself extends along the margin or surface of the part that bears it, and the mechanism of dehiscence does not involve a change of form of the sporangium, these arrangements have survival value, and are particularly favourable for the nutrition of large

sporangia with a large individual spore-output (Figs. 299, *A, B*, 301). But where the sporangia are separately attached to a flat central receptacle, and the mechanism depends for its efficiency upon elbow-room prior to the jerk of ejection, there will be space only for a few sporangia upon a central or linear receptacle (Fig. 348). If the number be increased a deadlock will ensue, and some of the sporangia may fail to eject their spores (Fig. 349). A change in form of the receptacle would resolve the difficulty. An early and very simple device has been its extension outwards from the point of attachment, whether this be from the margin of the leaf or from its surface. The former is characteristic of the *Marginales*, e.g., the *Dicksonieae*, and *Hymenophyllaceae* (Fig. 309); the latter of the *Superficiales*, e.g., the *Cyatheaceae* (Fig. 315). By this means several biological advantages are gained. The receptacle extends by more or less marked intercalary growth, and is traversed by vascular tissue: it thus gives space and nourishment for an added number of sporangia. The oldest of these are naturally those that are distal, and of those formed in basipetal succession below them the youngest will be nearest to the source of supply; these will also be the best protected, particularly where there is a basal indusium. Further, by adjustment of the annulus in an oblique plane the spores of those maturing in succession may be discharged without disturbing the rest (Fig. 310). Such biological advantages have confirmed the hold of the basipetal sorus among Ferns occupying a middle position in Descent, and those which possess it have been grouped organographically, though not along strict phyletic lines, as the *Gradatae*.

The gradate sorus spreads the call for nourishment of the successive sporangia over a prolonged period of development; and in this it is a biological advance on the simple sorus, where the call is simultaneous from all its sporangia. But this is not the only way of securing that advantage. A further amendment, which has a like effect, is that of interpolating an unlimited succession of younger sporangia between those formed earlier. This is characteristic of the most advanced *Leptosporangiate* Ferns, which have been styled collectively the *Mixtae*: the condition of the sorus which they present is that which is habitual in Ferns of the present day. It has originated polyphyletically, and may have been adopted as an amendment on either the simple or the gradate type. In the latter case there will be no need for a long receptacle; indeed it is found, whether in marginal or superficial sori, that the receptacle becomes flattened as the "mixed" condition is assumed: for instance, in the transition from the *Dicksonioid* type to *Hypolepis* or *Davallia* (Figs. 307, 311), or from the *Cyatheid* type to the *Dryopteroids*. With this goes also an extension of the receptacular area, which is particularly favourable where the sori are borne superficially on the leaf. It has the effect of extending the nutritional surface, and of bringing a larger number of the young sporangia near to the photosynthetic supply. Moreover, soral fusions

are frequent, sometimes marginal but often superficial ; while vascular commissures and vein-fusions underlie these coenosori. These features again aid nutrition : they have been specially described in Chapter XVIII. Thus the limits between individual sori are apt to be broken down, and the state described as "Acrostichoid" is finally reached, where large areas of the fertile blade are covered by a continuous sporangial field (Figs. 324, 325). Thus by gradual steps, not restricted to any one phyletic line, the identity of the sorus is liable to be obliterated ; but the origin of all such states may be referred by comparison to sources where the sorus was a definite unit :—as it is seen to be in the *Simplices*, or in the sporangiophores of the Microphyllous Pteridophytes. In this way the latest results of Pteridophyte-Evolution may be linked ultimately with a thalloid ancestry, but with the distal twigs fertile, and condensed.

These highly derivative conditions are found chiefly but not exclusively among the Ferns where sporangial interpolation is present. Crowding of the sporangia in the sori of most of the advanced Ferns makes a readjustment of the annulus necessary. The oblique position is effective for the *Gradatae*, but it would be mechanically inconvenient where the receptacle is flat. Hence the sporangia of the *Mixtae* have habitually a vertical annulus, which secures a free upward dehiscence for each individual in the crowded sorus. That this is a derivative state is shown by many intermediate steps, which lead to the final interruption of the continuous ring at the insertion of the sporangial stalk (Chapter XX).

Increase in the number of the individual sporangia in the more advanced Ferns is followed as a rule by a diminution of the number of spores produced by each ; but there is also greater precision in the mechanism of their ejection. The facts relating to spore-output are given at length in *Ferns*, vol. i., pp. 261-7, and in more condensed form in Chapter XX, p. 425, etc., of this book. The scaling down of the individual spore-output, on passing from the relatively large and prolific sporangia of the primitive Eusporangiates to those of the most advanced Leptosporangiates, is from thousands to units ; but yet the total spore-output remains high. In a well-grown plant of the Male Shield Fern it may be about 50 millions in a season : the number of the sporangia more than balancing the fall in output from each. The biological advantages thus gained by the later mode of development lie in the spread of the drain of nutrition over a prolonged period, the longer season of their supply as viable germs, and the more precise method of their dissemination. In these features the homosporous Ferns far exceed any other living Pteridophytes. The success of their method is shown by the many genera and species now living, and their wide spread in suitable habitats. This is all the more remarkable because each spore bears within it a very small nutritive supply, and the risks to which the sporeling is exposed are high. It is chiefly the enormous numbers in which the spores are produced

and the prolonged period of their distribution that counterbalance these dangers.

Lastly, there remain the protective flaps, of various form and origin, collectively included under the name of "Indusium." These have been described at length in Chapter XVIII. It appears that they are widely polyphyletic, and that they are of relatively late and superficial origin from the cladode. A marked exception is the indusium of the Blechnoids, which represents the curled leaf-margin (Fig. 319). Since ordinary indusia spring from surfaces of the cladode previously untenanted they will rank as enations. Their inconstant occurrence contrasts with the constancy of the sporangia which they protect. Indusia are not essential, and primitive sori may consist merely of a receptacle bearing sporangia. A parallel may be drawn between primitive sporophylls bearing non-indusiate sori and certain microphyllous strobili where the sporangiophores may be present without bract-scales. *In fact, the sorus of Ferns, though subject to wide variations of structure, is in its ultimate origin and constitution comparable with the sporangiophore of Microphyllous Pteridophytes, both of them being of the nature of condensed fertile twigs.* In either case the fertile twig may be *monangial*: either a sorus or a sporangiophore may bear only a single distal capsule. It may not yet be possible by close comparison to trace the individual sporangium of any Pteridophyte from a common source with the distal capsule of any Bryophyte; but they share originally the same position and function, and have a like place in the successive events of the alternating cycle.

The apparent divergence of constitution of the plant-body between the Microphyllous and the Megaphyllous Pteridophytes is apt to disguise the comparison between sporangiophores and sori. This arises chiefly from the difference in incidence of the photosynthetic function, which is not related constantly to any given part, while it involves changes of form and proportion. In such microphyllous types as the Lycopods and Calamites the nutritive function is chiefly carried out by the microphylls, though in a minor and varying degree also by the axis. The result is a photosynthetic shoot of which the leafy component may or may not be continued into the strobilus. In the megaphyllous types the nutritive function devolves wholly on the cladode leaf, with its distal forkings, and webbed expansion to form the blade. This may, however, be protected by enation-growths: these are developed as non-photosynthetic appendages. These differences in incidence of the nutritive function, which have influenced the form of the microphyllous and megaphyllous types, date back far in evolutionary history. But they mark no absolute distinction. In neither case are the more primitive types of spore-bearing members necessarily associated with enation-appendages: there are, for instance, bractless fertile twigs, as in *Zosterophyllum*, *Asteroxylon*, or *Archaeocalamites*, on the one hand; or, on the other, non-

indusiâte sori, as in *Stauropteris*, *Zygopteris*, or *Osmunda*. If we imagine all accessory parts—such as the microphylls of Lycopods, Sphenophylls, and Equiseta, or the ramenta and indusia of Ferns—as non-existent, and concentrate attention on axes and cladodes, then the comparison of sori and sporangiophores will appear in a clearer light. It is thus that the simple and archaic examples above quoted give a key to the fundamental comparison between the sporangiophores of the Microphyllous and the sori of the Megaphyllous Pteridophytes, notwithstanding the different position in which they respectively appear upon the vegetative system in relatively advanced types. Such ultimate comparisons are based upon the principle that, in the interpolated sporophyte, spore-producing members that are of primary origin take precedence, in morphological rank, over those that are vegetative and in various degrees accessory.

If on such grounds as those here explained the “simple” sorus of Ferns be accepted as a correlative of the sporangiophore of microphyllous types, the conclusion which Kidston and Lang drew for the Equisetales and Sphenophyllales may be further extended into the thesis:—that *the spore-producing parts, whether in microphyllous or in megaphyllous Pteridophytes, represent the persisting remains of the thalloid branch-systems found in some of the oldest Land Plants, viz., the Mid-Devonian Psilophytales*.¹

¹ Kidston and Lang, *Trans. R.S. Edin.*, 1921, p. 850.

CHAPTER XXX

ORGANOGRAPHIC ANALYSIS OF THE SPOROPHYTE OF THE ARCHEGONIATAE

IN order to form an opinion on the probable origin of a Land Flora we naturally turn to those plants of definitely sub-aerial organisation which, on a basis of wide comparison, are held to be lowest in the evolutionary scale. The old belief that this place is filled by the Archegoniatae, or "Higher Cryptogamia" as they used to be called, is still less open to doubt to-day than it was in the time of Hofmeister. It is now confirmed by positive fact in the discovery and detailed elucidation of fossils corresponding in many essentials to the living Archegoniatae: and these inhabited the earliest exposed land-surfaces for which the vegetation is recorded in detail. These fossils present features which help materially to consolidate such knowledge as follows from the study of Archegoniate Plants now living. It is easy to give *primâ facie* assent to such a general statement as this. But before that assent can be held as scientifically justified it will be necessary to examine critically the foundations on which the reasoning has been based. More particularly will this be desirable if the attempt be made to trace upward sequences from those held as primitive.

In all such constructive essays it is necessary to keep the distinction clear between hypothesis and demonstration. The latter is rarely possible except among organisms closely akin: the further apart in character the organisms compared the more doubtful any opinion is bound to be as to their relation by descent. Still such hypotheses are necessary if wide comparison is to exist at all; their use is a legitimate method in morphology. Evolutionary views themselves are no more than working hypotheses; for instance, the belief that all Bryophytes are in one form or another related by descent; or that the extinct vascular plants of the Rhynie Flora form a valid bridge morphologically between Bryophytes and Pteridophytes, appear inherently probable. There can be no objection to such working hypotheses as these, provided they are not stated or accepted in place of demonstration. These general ideas form a cautionary introduction before making use of the facts and arguments of the foregoing Chapters in any statement of views as to the Origin of a Land Flora.

GUIDING PRINCIPLES

In order to be clear as to the methods used in handling the observational material certain guiding principles may be laid down, which will serve to lead the discussion into correct channels :—

(I.) An *upward outlook* is in itself a practical application of any evolutionary view. This seems like a platitude to-day ; but it is not difficult to quote from current literature instances where it has been neglected. It is not only in the “ Nature Philosophy ” of a former century that organisms lower in the scale have been interpreted in terms of the higher (Chapter XXVII). Recent discussions on the fertile twigs of the Psilotaceae afford examples of rendering them in terms of leafy shoots, based on the definite categories of axis, leaf, and sporangium ; they should, however, be analysed rather as shoots not yet fully differentiated, with features possibly of indeterminate character. Parts do not as a rule originate with full characters that consign them to one category of parts or to another ; but in accordance with the conditions to which they are exposed they have in the course of their evolution gradually acquired such characters as to justify their being so ranked for purposes of description or comparison ; for instance, the axis and cladode leaf. Categories are a human device for convenience in collective handling. Organs need not conform *ab initio* to one or to another. The lower in the scale the object studied the less the degree of conformity may be expected to be.

(II.) A wide latitude must be given for *homoplastic origin* of parts, and of their characteristic form. Homogeny can at most be securely asserted only in circles of near affinity and, in its strictest sense, only in the early stages of development of such individuals as are endowed with a continued embryogeny, as the higher plants habitually are : such homogeny as is exemplified by the hand of a mother and of her child.¹

(III.) *Precedence in comparison should be given to normal over abnormal development* (Chapter XXIV). Again this seems like a platitude, but in discussions on Alternation a large place has been given to aberrant and even isolated results of development, over conditions that recur in such an overwhelming majority of individuals as to merit their acceptance as the normal. It is sufficient to mention the names of Apogamy and Apospory. These take their proper place as illustrating present possibilities of development ; but they cannot rightly be assumed to supersede the events of that cycle which is normal, in the sense that its events are regularly present in the vast majority of species and individuals grown under average conditions. The fact that in that cycle modern variants may exist in Nature, or be produced experimentally and at will, does not suffice to justify for them any priority of

¹ See Address to Sec. K., Brit. Assoc., *Report*, Bristol, 1898, where different degrees of correspondence are discussed on the basis of Ray Lankester's analysis (*Ann. Mag. Nat. Hist.*, vol. vi., p. 34).

importance as history ; for who is to know that the conditions of life in the open, or of experiment, or even of the subject of experiment itself, are the same to-day as in that remote past when what is held to be normal was evolved ?

(IV.) Specialised parts are commonly derived from pre-existent parts not so specialised. This statement is trite enough ; but it is liable to carry with it a presumed improbability that new parts may originate where none existed before ; or at least that this is rare, and that the parts so formed are essentially of lower morphological grade. The upward point of view would discourage any such presumption, particularly where primitive organisms are concerned. These should be held as possessing indefinite rather than definite possibilities. For instance, though megaphylls may be traced comparatively from dichopodial development of distal forking, it does not follow that all parts having the dignity of leaves are necessarily of distal origin by forking. *The enation of new parts from an embryonic surface not previously tenanted should be held as possible even in plants already showing distal forking* ; also that the enations may spread to regions of the primitive plant previously without them, and take up various functions, whether protective, secretive, or photosynthetic. For instance, parts originating as innovations may gradually have attained full rank as leaves, whether morphologically or functionally.

(V.) *The function of photosynthesis is not restricted to any definite part or parts of the plant, however usual it may be that such localisation should exist.* This is a commonplace of comparative morphology for the higher plants, as is also the conclusion that a part commonly photosynthetic may cease to be so. The converse, however, that photosynthesis may be assumed by a part previously non-photosynthetic is less familiar. Instability of localised photosynthesis seems specially marked where the form is relatively simple, as in the Bryophytes and primitive Pteridophytes. Two examples may be cited from Archegoniate plants : one is the specialised enlargement of the apophysis in the Splachnales, or of part of the sporogonial wall in *Buxbaumia* ; in both there is localised photosynthesis, though without the formation of definite appendages. The other is in the Psilophytales, where appendages that appear to be of the nature of enations are sometimes spinous, but frequently photosynthetic. These share with the microphylls of the Lycopodiales and Equisetales a wide latitude in the incidence of photosynthesis. But parts of corresponding position, such as the hairs, bristles and scales of the Filicales, are for the most part non-photosynthetic. Such differences show how variously the nutritive function fits upon the morphological framework in primitive plants. This fact requires to be taken fully into account in their comparative treatment ; for the localisation of photosynthesis does not determine the origin of parts, though it tends to mould them.

(VI.) *Distal Fertility* is a natural consequence of segregation of the functions of nutrition and propagation, which however are not clearly differentiated in primitive plants: they may even be carried out by the same cell-unit in unicellular plants, such as the Desmids. But in all higher organisms these functions tend to be separated both in space and in time. Instances of progressive segregation may be quoted from both alternating phases of the Archegoniatae. In the gametophyte of the Anthocerotales the gametangia are scattered over the photosynthetic thallus, as is the case also in most of the Pteridophytes; but in that of the Marchantiales, and in the higher Bryales, the distal segregation of a fertile region from the photosynthetic may be such as to bear comparison with that seen in the sporophyte of Flowering Plants. In the sporophyte of the Archegoniatae it is often possible to trace by comparison, or even in the individual ontogeny, how *sterilisation of fertile cells* plays an important part, being often so localised as to leave only a distal region fertile. Such segregation of the nutritive and propagative functions is imperfect in the sporogonium of the Anthocerotales; but it is a marked feature in more advanced Bryophytes, while there is a complete absence of photosynthetic tissues in the sporogonia of most Liverworts. In these and the Mosses the spore-production is deferred: and this is so far characteristic for them and for primitive Pteridophytes as to justify the apposite title of "*Telome*," introduced by Zimmermann, to connote that unit or part which ends normally in a distal capsule (see p. 617). *All such states follow from the fundamental fact that nutrition must necessarily precede propagation, whether the source of the nourishment be from the parent gametophyte or from the sporophyte itself.*

(VII.) *Elaboration of Form tends to follow on increase in Size.* This is a fact of general experience: it culminates in dendroid vegetation with its elaborate branching and numerous leaves. In order to realise the initial steps in attaining this state reference must be made not to Flowering Plants or even to Tree Ferns in their adult state, but to primitive types, and particularly to their ontogeny. The primary development of Archegoniate Plants, whether of their gametophyte or of their encapsulated sporophyte, starts from the spore or from the zygote, either of which is approximately spherical; and this habitually passes to a more or less *obconical form*, enlarging upwards. Here we trace the consequence of the fundamental fact that plants are accumulators of material rather than expenders, which leads naturally to increase in size. *Sooner or later, and in more or less marked degree, an obconical form is assumed in all plants of continued growth and of normal primary development; whether in the gametophyte (Figs. 96, 204), or in the sporophyte (Figs. 225, 266).*

An inevitable consequence is that, as size increases, provided that the form be retained as before, the bulk would increase as the cube, but the surface only as the square of the linear dimensions. The result of increase

in size without change of form would lead to progressive disproportion of surface and bulk, and consequently to physiological inefficiency : but any elaboration of form would tend to meet the difficulty. This *Theory of Size and Form* has been stated for the primary conducting tissues in Chapter XXVIII ; but it applies equally to all limiting surfaces of the plant. Hence as regards the external surface the larger the plant or part, the more elaborate its " presentation surface " should be, whether this be carried out by external moulding, or by internal channels of ventilation, or by a combination of both. The Archegoniatae illustrate both of these methods, and in the sporophyte they are habitually combined ; but in the gametophyte they are not. Hence it is in the latter that the simplest examples may be expected. Moreover, the gametophyte develops freely exposed, while the embryo of the sporophyte is encapsulated ; a circumstance which tends to more clear demonstration of the principle in the former.

Examples of young obconical gametophytes are seen in the following illustrations. The simplest method is by flattening of the obconical body to form a thin expanse, as in *Sphagnum* or *Tetraphis* (Figs. 39, 55) ; or in the prothalli of Ferns (Figs. 364, 392). The same end may be reached by filamentous branching (Figs. 366, 390). Where the form is more definitely obconical it may be by internal ventilation (Fig. 391), or by the formation of lobes (Figs. 146, 200, 395). These may all be held as homoplastic responses by elaboration of form to meet the same fundamental need, of maintaining a due proportion of surface to bulk in a body enlarging upwards.

In the evolution of the Sporophyte two chief methods are primarily involved, viz. : (i) distal forking, and (ii) enation, while internal ventilation takes a prominent place.

The statement of these principles and conclusions (I.-VII.) will lead towards a plastic view of the primitive constituents of a Land Flora, and particularly of their sporophyte. Each individual may be regarded as an organogenic experiment, with a more or less definite bias towards certain inherited modes of development. But the result of each experiment is dependent in varying degree upon the conditions of its growth, which tend to modify the inherited tendencies. This view as applied to relatively primitive types will probably lead to a better understanding of the adult than any attempt to classify its parts according to preconceived categories. Its effect would be to find the members of the relatively primitive archegoniate plants in a nascent state, imperfectly organised and generalised in type. They would appear as in an upward scale of development rather than reduced. In fact, the outlook would be the converse of that reflected in the pre-evolutionary Nature Philosophy. So far as categories of parts are recognised, these should be built up inductively from below, having regard to all the

conditions of development, past and present. Among those conditions the Size-Relation should now take its place. Its influence is insistent and inevitable over every enlarging organism, and has been specially effective in its moulding action during primary development.

The Nuclear Cycle, with its alternating events of syngamy and reduction, forms a normal foundation for the life-history of all organisms that possess sexuality. (Introduction, and Chapter XXIV). All the Archegoniatae have grasped the two opportunities presented by that cycle for somatic development: they possess both a haploid phase in the gametophyte, standing between meiosis and syngamy; and a diploid phase in the sporophyte, that falls between the events of syngamy and meiosis (Fig. 2). But as they are seen to-day they give no direct evidence how that condition came about; nor is the relation of the Archegoniatae sufficiently close with any Class of Algae to resolve the question with certainty by the aid of comparison with them. Alternation here stands as an accomplished fact. Nevertheless, for reasons advanced in Chapter XXV, it appears that a near comparison with organisms now living would lie with certain Isokont Green Algae; whether in point of habit or habitat, or of photosynthetic equipment, or of the type of the gametes. These plants are already advanced to the state of oogamy, and in common with many other Algae they are *haplobiontic*, possessing no pluricellular sporophyte. Such comparisons give reasonable ground for the opinion that the Archegoniatae may have sprung from some type or types of green haplobiontic organisation, of littoral and probably fresh-water habitat; and that in their evolution the gametophyte existed as a somatic body before the sporophyte acquired a pluricellular state. But however cogent this view may appear, the question has to be decided for the Archegoniatae on their own merits, though with the knowledge that a sporophyte has originated also in widely different plants of Algal nature. The alternate phase in Red and Brown Algae may accordingly be held as homoplastic with that of the Archegoniatae, and the general conclusion will be that in various conditions of life a diploid phase is an advantage, and has been secondarily achieved.¹

The normal facts of structure and ontogeny of the sporophyte in the Archegoniatae being consistent with a view of its origin by interpolation between successive gametophytes, as a new somatic phase, it has been shown how a nascent sporophyte would possess special survival value for life on land. It would afford the opportunity for an increasing number of nuclear combinations; the supply of numerous air-borne spores would favour the spread of individuals, and there would be relief from dependence on re-

¹ The question of the bearing on this of the irregularities known as Apogamy and Apospory has been dealt with in Chapter XXIV, and the view was there adopted that they are *ex post facto* events, while the morphological basis of Archegoniate alternation is the normal nuclear cycle.

peated syngamy for multiplication. These considerations suggest that *the survival value of a neutral phase in Land Plants would be such as to stabilise it biologically when once in being*. If the new soma were itself independent and photosynthetic the circumstances would appear favourable for a large spore-output in sub-aerial life, provided the sporophyte could tide over the initial stages of germination, and acquire the necessary food-material.

It is here that the most characteristic features of the Archegoniatae come in, in the form of the protective archegonium and within it the embryo, which is constantly a three-dimensional body after the first developmental stage is past. The uniformity of these features in large and varied classes of the Archegoniatae points to their importance in relation to a land-habit. It is the protective archegonium that makes the establishment of such a sporophyte possible on land. Among the green fresh-water Algae of littoral habit protection of the fertilised egg is not unknown; for instance, in *Chara* and *Coleochaete*. But their state is rudimentary, and differs so far in detail from the stabilised protection and nursing seen in the Archegoniatae as to suggest for each an independent response to similar conditions.

The first step in the formation of an interpolated diploid soma would involve a delay of meiosis by *sterilisation* of a cell normally fertile; and the process would be liable to be repeated in later divisions. We have seen in Chapter XXIV how a theory of sterilisation accords with Naegeli's fundamental law of organic development, and that the probability of its truth is witnessed by many detailed instances in more advanced stages of the sporophyte.¹ There may have been some difficulty in the first step of such sterilisation, and this may account for the survival of haplobiontic Algae, in which it is absent. But in view of the frequency of the event in later phases of the sporophyte of land-plants, there seems in them to be no initial objection to that step of sterilisation which has paved the way to the biological advantages above noted. It may be held as an open question whether the sporophyte thus interpolated between syngamy and meiosis was originally free-living, or encapsulated from the first, as it is always in the Archegoniatae—with obvious biological advantage for land-living plants. This is, as Von Goebel remarks, an academic question so long as experimental facts are wanting. But from embryological comparison a filamentous structure appears to be initially probable, though the circumstances of internal embryology are such as to encourage a massive, three-dimensional structure of the embryo before it emerges from the venter; and biologically this would be important in the establishment of the young sporophyte as an independent sub-aerial plant.

Such is in brief outline the interpolation-theory of alternation here adopted. It is substantially the same as that stated in *The Origin of a Land Flora*. It reads the facts of the normal cycle into a biologically reasonable history of the origin of Primitive Plants of the Land; and it is retained for them

¹ *Land Flora*, chap. vii.

notwithstanding many later-acquired details for Algae. This accords with the final conclusion stated by Von Goebel, that the doctrine of alternation, founded originally for the higher plants, from the Bryophyta upwards, cannot be extended to all plants.¹ Alternation in the Land Flora is a phenomenon that must be studied on its own merits: the conditions under which it developed having tended to stabilise in them a more consistent succession of events than in the Algae, where such influences are not present.

In the further course of this discussion the gametophyte will almost drop out of sight. Its organography shows points of similarity with that of the sporophyte; but this is natural enough since both are parts of the same organic cycle, and they develop subject to conditions essentially the same. The incidence of these is less drastic for the low-growing gametophyte than for the erect sporophyte; consequently it is less standardised in form in relation to them. But in the ascending and upright types of gametophyte the soma as it increases in size secures a due proportion of surface to bulk by elaboration of form. Often this is irregularly lobed as in the prothalli of *Lycopodium cernuum* or of *Equisetum*. It is only in the gametophyte of the leafy Liverworts and Mosses that there is a high degree of standardization of the leafy shoot, though without internal ventilation. Such results are of interest in the present organographic discussion chiefly because they illustrate, in gametophytic plants which cannot by any stretch of imagination be referred to a telomatous origin, that a foliar development may arise by enation, analogous to that seen in the origin of the microphylls of the sporophyte.

TELOMES

The introduction of the term "Telome" by Professor Zimmermann has clarified the morphology of the sporophyte in the primitive Archegoniatae; the conception of it as a constructional unit may be applied generally to the vegetation of the Land. But the recognition of that unit will naturally become more difficult as the complexity of structure increases. In view of the importance of the unit thus named a brief abstract may be given of Zimmermann's original text, but without signifying adherence to the details of its application.²

The whole wealth of form that characterises living Cormophytes is reducible to one fundamental organ, the "*Telome*," which consists of a distal sporangium and a stalk usually with vascular supply (Fig. 445). Such organs may be linked together in various ways to form complex plant-bodies. In these the common term is applied to the last branchings of twigs or shoots, so far as they are uniaxial. Each of these presents the morphological unit of the Cormophyte shoot. Each one ends downwards at the point of junction with another telome. The coalescence of telomes constitutes a "*syn-telome*."

¹ Von Goebel, *Organographie*, Teil i., 1928, p. 526.

² *Phylogenie der Pflanzen*, Jena, 1930, pp. 58-70.

Fertile telomes may be called sporangia: where grouped they form fertile *telome-trusses* (*Telomestände*). Alternatively the neutral designation *sporangial trusses* (*Sporangienstände*) may be used, and these may be differentiated as sporophylls, or as flowers. Sterile telomes are designated "*Phylloids*," and those united phylloids from which sterile leaves and axes have been differentiated are called *phylloid-trusses* (*Phylloidstände*). Naturally there are mixed telome-trusses which comprise both sporangia and phylloids: the similar arrangement of these parts clearly demonstrates their original homology. The great majority of fern-sporophylls and of flowers of Angiosperms are such mixed telome-trusses.

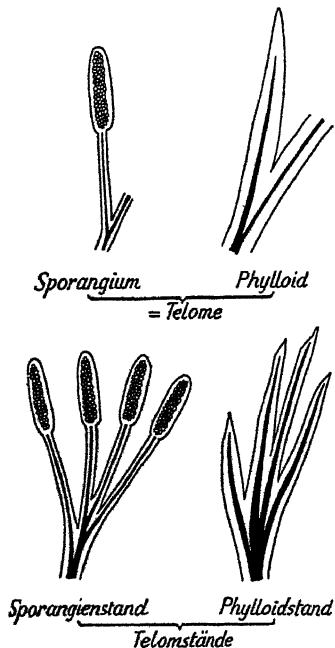


FIG. 445.

Diagrams of "Telome und Telomestände," after Zimmermann; fertile to the left, sterile to the right.

Zimmermann raises a warning against too rigid an application of the definition of the telome. For instance, referring to emergences he remarks that the delimitation of these from telomes is not easy: in principle perhaps impossible. Foliage leaves are the last branchings of the phylloid truss. These may be developed in two different ways: either each one directly as a more or less flattened expansion to form a single-nerved needle, as in the Equiseta, Lycopods, and Conifers (*microphyll*); or a number of phylloids of a phylloid-truss may unite to form an expanded foliage-leaf (*megaphyll*). He contemplates a series of elementary transformations in the phylogenetic origin of megaphylls (*l.c.*, p. 68), such as *overtopping* (Uebergipfelung), *webbing*, and *transition from three-dimensions-branching to a single plane*; in fact, such changes as have been described in Chapters XVI and XXVII.

As to the relation of the sporangia to the sporophyll he recognises four different states (*l.c.*, p. 69): (a) the primitive distal and erect position, as in *Rhynia* and other ancient types; (b) the sporangia pass (*rücken*) to the leaf-axils, as in the *Lycopods*; (c) they are transferred (*verlagert*) from the margin to the surface of the blade, as in *Ferns*; or (d) they may become pendulous, giving the peltate sporophyll, as in *Equisetum*.

Lastly, as to the origin of roots, he remarks (*l.c.*, p. 70) that we may assume these to have originated phylogenetically from creeping shoots before the differentiation of leaves.

The analysis of the Cormophytic plant, based upon Zimmermann's scheme here briefly sketched, is not in full accord with certain facts and arguments advanced in this work. It has been introduced here partly as a

basis for discussion, partly because of the value of the fundamental conception of the "telome." In view of the closer linking of the Bryophytes with the Pteridophytes, which naturally follows from facts recently disclosed, it would seem natural to rank their sporogonia, and particularly those of the Anthocerotales, as simple types of telome. The occasional introduction of a new term may have the effect of crystallising out a large body of facts previously floating freely: as, for instance, when Strasburger produced his synthesis under the title of "Periodic Reduction." So now the conception of the "telome-unit" tends to clarify the relation of many floating facts already used comparatively, but without linkage by specific designation. The fact of distal fertility in the primitive sporophyte is familiar enough; it follows as a natural consequence of the dependence of propagation on antecedent nutrition. The term *Telome* stamps that physiological fact as a wide organogenic feature. (VI. above).

Exception may be taken to Zimmermann's designation of sterile telomes as *Phylloids*. It is explained that foliage leaves are the last branchings of a phylloid-truss, and that they develop in two different ways: either each phylloid forms directly a flattened, single-nerved needle, as in the *Equiseta*, *Lycopods*, and *Conifers*—the *microphyllous type*; or many phylloids of a truss together form a large-bladed foliage leaf—the *megaphyllous type*. His view appears to be that microphylls and megaphylls are of like origin, both representing sterilised telomes, and differing only in the number of phylloids involved. Even if this were so it would appear advisable to assign to the smaller types of leaf, as in *Equiseta* and *Lycopods*, some new and distinctive term, such as "telophylls." This would leave the use of Lignier's generally accepted word "microphyll" untouched; and the place and manner of their origin unrestricted. Though in its detailed application the telome theory does not wholly accord with the facts cited or the views expressed on strobili and microphylls in Chapters XXVII and XXIX, it has a definite value in relation to the origin of megaphylls, and of the sori which they bear. It also gives a very natural aspect to sporangiophores and synangia. But the attempt to extend it so as to account for the origin of microphylls in general as non-fertile telomes does not carry conviction. In the pages which follow an alternative interpretation of their origin will be advanced.

The conception of the fertile *Telome* involves a single distal sporangium borne upon a simple stalk, which is traversed by a conducting strand. It is based by its author upon analysis of the shoot as seen in *Cormophytes*, which are held to be built up from such units. Each telome presents the morphological consequence of segregation of the nutritive from the propagative function, the latter being naturally distal. With this segregation already achieved, enquiry may extend downwards to simpler states, or upwards to those more complex. The sporophyte either of the simpler Bryophytes or

of the more complex Pteridophytes may be considered in terms of the telome. This alternative application appears justified by broad comparison of these two divisions of the Archegoniatae.

Following the facts and arguments adduced by Campbell and Von Goebel, the Anthocerotales appear among living plants as the nearest approach to a synthetic type between Bryophytes and Pteridophytes (Chapter I). In their sporogonia the segregation of the nutritive and propagative functions is imperfectly carried out. This suggests a common source for the distal sporangium and its stalk: in fact, it may be held as representing a telome in the making, the diploid phase being seen in a state prior to the differentiation of the capsule and the stalk. In the Sphagnales and Andreaeales there is a clearer distinction of these parts, while the Bryales present the capsule in its highest specialisation (Chapters V, VI). But the sporogonia even of the most highly advanced Bryophytes are deficient in certain features that are essential for further advance as Land Plants. We see in them how a great Class may make the best of the sporophytic unit which underlies the larger development of Vascular Plants. Beyond this consolidation of the idea of the Telome the Bryophyta give little direct help in building up a conception of the more complex body seen in the Pteridophyta.

Some of the simplest and earliest Vascular Plants lend themselves readily to interpretation in terms of telomes only. It may remain uncertain whether or not *Sporogonites* will finally turn out to be a simple telome of a Bryophyte type; or that specimens hitherto in hand are isolated branches of a more complex system. But the plant as it stands, whether from Scandinavia or from Australia, is certainly suggestive of the former. In any case its capsule was distal and erect (Fig. 439). The same holds for the Rhyniaceae; but here the branching of the leafless shoot is dichotomous, with a tendency to sympodial development (Fig. 78). Not infrequently two sporangia may be borne side by side on a forked stalk, or even a double sporangium may be seen, as in *Hornea Lignieri*, suggesting that the bifurcation has occurred within the limits of the sporangium itself.¹ Further, though in *Rhynia* no columella is present, in *Hornea* a sterile tract is found rising like the columella of Bryophytes from the base of the capsule (Fig. 441). Thus in the Rhyniaceae we see free land-living organisms which bear distal sporangia having certain Bryophytic characters; and that these are borne upon bifurcate vascular stalks. Such facts suggest that in very early time certain primitive land-plants were not restricted like the Bryophytes to a single telome, but found in repeated dichotomy a means of increasing their vegetative system, and their consequent fertility, by numerous telomes (compare Chapter XXIX, Fig. 440).

¹ A similar condition has been demonstrated in abnormal synangia of *Tmesipteris*, where the septum was incompletely formed (Bower, *Phil. Trans.*, 1894, B, Plate 52, Figs. 158-164, pp. 545-7. Also in *Brotrychium*, p. 364, Fig. 298.

A particular interest attaches to those early fossils in which the sporangia are so disposed upon a leafless axis as to suggest its dichopodial development. Examples are seen in *Hostimella racemosa*, and in *Zosterophyllum* (Fig. 446).¹ In both an equal dichotomy is characteristic of the vegetative region; but the fruiting branches, each terminated by a sporangium, are compacted into a lax type of strobilus, and so disposed as to indicate a sympodial system, of which each branch is itself a telome. On the other hand, *Hicklingia Edwardi* presents a simpler condition where each elongated stalk ends in a single sporangium, as in the simplest of the Psilophytales.² The result of these comparisons is to visualise, in known plants of Devonian age, various steps intermediate between the simple telome and a leafless strobilus composed only of telomes grouped sympodially.

The Class of the Lycopods stands apart in the fact that their cones are composed of solitary sporangia of the type seen in *Zosterophyllum*, but each is associated with a bract. In other Pteridophytes a plurality of sporangia are borne upon a common stalk, as in the sporangiophore of microphyllous or in the sorus of megaphyllous types. By consent, which is rapidly becoming general as the number

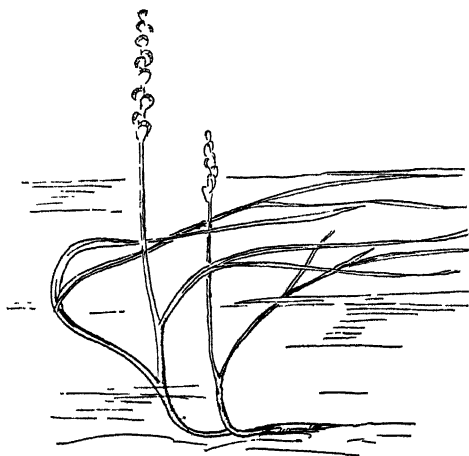


FIG. 446.
Zosterophyllum rhenanum, Kr. and Wld., from Lower Devonian of Wahnbachthal, near Siegburg. Reconstruction by Weyland. (About natural size.)

and variety of known fossils is increased by new discoveries from ancient horizons, such groups of sporangia may be regarded as condensed "telome-trusses." They are borne either on a relative main axis to form a strobilus, as in *Equisetum* or *Sphenophyllum*; or on a cladode, as in the Ferns. The isolated sporangia, sporangiophores, or sori are usually associated with vegetative organs: these appear as bracts or as indusial growths, and they serve various purposes such as photosynthesis, protection, and probably also of ventilation of the underlying tissues. In the variety of their relation to the spore-producing members these have presented difficult problems of comparison. But one historical point is constant for them all. Spore-production has in Descent been the first office of the sporophyte, though in the individual

¹ Lang, *Trans. R.S. Edin.*, 1925, vol. liv., Plate iv. Also *Phil. Trans.*, 1930, B, vol. 219, Plate 12, Figs. 16-20.

² Lang, *Trans. R.S. Edin.*, 1923, vol. lii., p. 405.

plant it may appear as the final result. Hence the telomes, of whatever form, are to be held as *primary*: all the rest are accessory, and in ultimate origin *secondary*. That they are so is indicated by the early existence of lax and bractless fertile branches in the Rhyniaceae, in *Hostimella*, and in *Zosterophyllum*; with which in this respect the bractless cones of *Archaeocalamites* and *Equisetum*, as well as the exposed sporangia and sori of the most primitive Ferns may be associated. *These early types uphold the priority of existence of the spore-producing members, and show the accessory nature of the appendages associated with them in later types.*

ENATIONS

The origin of an *enation* is *not distal but lateral*, and parts so produced are from the first appendicular. They are formed by outgrowth from surfaces previously unoccupied, and they commonly appear without any regularity as to the position, or even in some cases the time, of their appearance. Whereas the *telome* is *initially fertile*, bearing a distal capsule, the *enation* is *initially sterile*, and bears no distal capsule. Lastly, while the *telome* is of *primary origin*, preceding in evolution any other part of the sporophyte, *enations* are *secondary*, and originate superficially from telomes, or their derivatives. There is no sufficient evidence from living plants to show that enations at large are sterilised telomes: there are indeed many facts which make this appear improbable. Nevertheless it is not denied that sterilisation of telomes may have existed. This indeed appears to be suggested by certain fossils known only as impressions. But neither the *Thursophyton*-leaves of *Asteroxylon*, nor the spines of *Psilophyton*, nor yet the bristles of primitive Ferns, such as *Ankyropteris*, *Gleichenia*, *Loxsoma*, or *Dipteris*, can be referred to this source. Under the heading of Enations may be grouped hairs, scales, prickles, emergences, and small photosynthetic leaves. Hairs arise from a single superficial cell, emergences from a number of cells, some of them hypodermal: these may even include vascular tissues. Some are massive outgrowths, as in the armature of spines seen in the larger Ferns. Scales and stiff bristles are frequently present in early Coenopterid Ferns. Such enations may arise in the apical bud, together with the cladode leaves; but these are easily distinguished from them in an early state of development by structure and arrangement (Fig. 447).¹

The so-called *Thursophyton*-leaves of *Asteroxylon*, which are of the nature of enations, are specially interesting in their distribution, for they occupy only the robust middle region of the adult plant.² They have been shown to

¹ The scales of living Ferns have habitually been ranked as only a form of hairy covering; but as Hofmeister remarks "certainly a very highly developed one, as they frequently contain chlorophyll, for instance, in *Platynerium*" ("Higher Cryptogamia," Ray. Soc., p. 212, footnote).

² Fig. 449, and Frontispiece.

originate in acropetal order round the apex of the growing circinate shoot.¹ They correspond in position and in structure to the appendages of other Psilophytales, and to the microphylls of the living Psilotales; though here, as distinct from *Asteroxylon*, they are continued on to the fertile region, and appear in close and definite relation to the synangial trusses. On the other hand, they are absent from the basal region of the plant: in *Tmesipteris*, the only type of the Psilophytales and Psilotales in which the embryology is fully known, such appendages are altogether wanting in the embryo. These facts support the conclusion that the microphylls or *Thursophyton*-leaves are accessory appendages.² Wide comparison leads to the view that enations represent an upgrade progression from leaflessness rather than downgrade

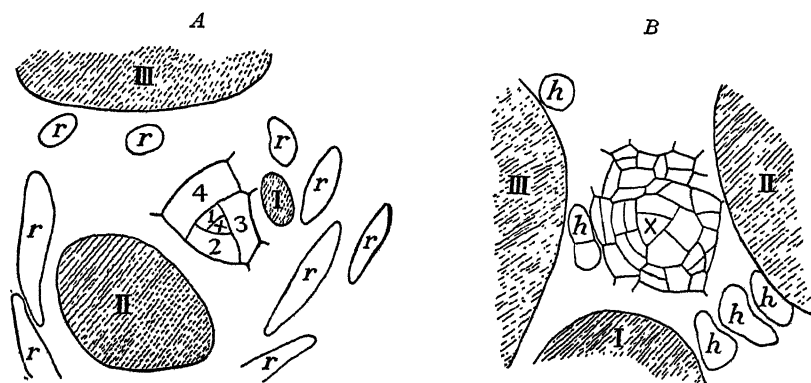


FIG. 447.

Semi-diagrammatic traces taken from photographs supplied by Dr. Lang, but with the segmentation accurately drawn; they show transverse sections of the apex of the shoot. A, of *Dryopteris filix-mas*. B, of *Osmunda regalis*. In both the cladodes, which are shaded, differ from the enations in size, in the details of their origin, and in their disposition. h=hairs; r=ramenta; A $\times 125$; B $\times 200$. Refer also to Fig. 255 for details of the cladodes and ramenta in *Polypodium*.

steps of reduction. That they are to be read as presenting appendages in various stages of advance from minute outgrowths to efficient photosynthetic organs (*Psilotum*), sometimes without vascular supply, sometimes with a conducting strand (Fig. 425). In other early types, however, they appear spinous; these compare with similar outgrowths at the leaf-bases of certain early Ferns, such as *Ankyropteris* (Holden, *l.c.*). Taken together, these various types of enation suggest tentative steps in development of parts not standardised in relation to any definite function, though often capable of photosynthesis. It is worthy of note that in point of distribution they show some degree of relation to the size of the part that bears them. In *Asteroxylon* they occur on the largest stems (Frontispiece). They may co-exist with fertile telomes, or they may be absent in plants not definitely strobiloid.

¹ Kidston and Lang, *l.c.*, part iii., Figs. 30, 36, 90. Also Zimmermann, *l.c.*, Fig. 49.

² For details see Chapters VII, VIII and XXVII.

The next step will be to consider the collocation of enations and telomes to form a compact strobilus.

There is no doubt of the supremacy of the definitely strobiloid habit in the Microphyllous Pteridophytes, over the early lax types, such as are seen in the fossils *Zosterophyllum* and *Hostimella racemosa*:—though the living Psilotales are still left as examples of a loosely built fertile shoot. A circumstance favouring the compact cone has been the advantage gained by mutual protection of the closely packed parts up to maturity, an end greatly advanced by the presence of bract-scales. A *radial symmetry* is prevalent among the microphyllous cones thus constructed: even in *Selaginella*, where frequently the vegetative region is dorsiventral, the cone reverts (with few exceptions) to the radial symmetry. This contrasts broadly with what is seen in megaphyllous types, with their flattened cladodes.

It has been seen in Chapter XXIX how the cone of microphyllous types consists of an axis bearing simple telomes (Lycopods), or telome-trusses (Psilotales, Sphenophyllales, Equisetales): and that in certain ancient types these are without attendant bracts (*Hostimella*-twigs of *Asteroxylon*, *Zosterophyllum*, *Archaeocalamites*): though more frequently bracts are associated with them (Psilotaceae, *Lycopodium*, *Calamostachys*, *Sphenophyllum*). Comparison indicates that those two types of appendage were diverse in nature and in origin. It thus appears that in the leading types of Microphyllous Pteridophytes the compact, radially constructed cone is a composite body involving an axis, simple telomes or telome-trusses, with or without enation-leaves. This constitution of the radial cone presents analogies with the disposition of the telomes (single sporangia) and telome-trusses (sori), with or without indusial protection, which are borne upon the dorsiventral cladodes of the Filicales.

CLADODES

The characteristics of the Megaphyll, or Cladode leaf, as seen in the Filicales, have been discussed in Chapter XXVII, together with its probable origin as a consequence of dichopodial development; while in Chapter XXIX its relation to the spore-producing members has been considered. As expressed in Telomes, the cladode probably originated in a three-dimensional system of these units, which was characterised by free forking both of the lower and of the distal twigs, while intercalary growth of their stalks will have been a prominent feature. Such a scheme is foreshadowed in its simplest form by the habit of the Rhyniaceae (Figs. 78, 79). A type with a high degree of ramification is seen in the restorations of the Coenopterid, *Stauropteris*, as shown in Fig. 448, p. 626. Here most of the distal ramifications were fertile, while photosynthesis was carried on, as in the Rhyniaceae, by the lower parts of these highly ramified telomes. They were cylindrical, a

sheath of photosynthetic tissue surrounding the central conducting strand. There were no expanded leaf-blades in *Stauropteris*, and it is doubtful whether there was any rhizome. In the leaves of the typical Ferns, however, the branch-system is two-dimensional; and this, combined with partial or complete sterilisation of the telomes, and "webbing" by lateral fusion of the contiguous segments ("telophylls"), led readily to the flattened expansions characteristic of later types. These at an early stage took the form of fan-like or pinnate blades, the radiate forking of the veins indicating their origin by webbing of the original units. Parts thus referable in origin to a coalescence of bifurcating telomes, all potentially or actually fertile, constitute what are known as the Cladode leaves, or Megaphylls (Figs. 226-241, also Fig. 293).

The differentiation of Axis and Cladode leaf from an indeterminate dichotomy has been fully discussed in Chapter XXVII. The history of opinion in regard to the evolution of the megaphyllous shoot has there been traced from 1875 up to the demonstration of the Devonian land-plants by Kidston and Lang (1917-1921), and by Kräusel and Weyland (1926, etc.). These have provided the basis of observation which the earlier work lacked, viz., that plants existed in the earliest known land-flora with an indeterminate dichotomising branch-system, in which leaf and axis were not differentiated. These plants, and particularly the fossil described by Kräusel and Weyland as *Protopteridium hostimense*, Krejei (*Flora d. Böhm, Mitteldevons*, 1933), show those initial steps of dichopodial development that lead to the distinction of axis and cladode leaf. The general conclusion, suggested hypothetically in 1884, may now be stated as well founded in fact: viz., that *as dichopodial development in a dichotomising Fern-leaf is seen to lead by gradual steps to the production of lateral pinnae upon a rachis, so a like development in an indeterminate forking shoot is believed to have resulted in the production of cladode leaves laterally on an axis*. If this be so, then in megaphyllous shoots the stem, as such, would not have been pre-existent in the most primitive forms. It would actually originate as a *pseudo-axis*, built up from a succession of telome-stalks. But at a very early stage these would have been liable to abbreviation and distension, so as to form a continuous trunk upon which, as the development proceeded, the megaphylls would appear monopodially as lateral appendages. This history of the origin of the Cladode Leaf is thus quite distinct in its initial steps from that of the microphyllous or enation-leaf.

The relation of the Sporangia to the Cladode Leaf has been dealt with in detail in Chapters XVI, XVIII, and XXIX. Though in modern Ferns the number of sporangia is usually large, and their arrangement varied and complex, in the most primitive types the sporophyll and its sporangia are readily resolved in terms of telomes, each sporangium representing the distal head of one of these units, borne on a vascular stalk: a condition which is prefigured by the Rhyniaceae (Fig. 78), and elaborated in *Stauropteris* (Fig.

448). From the Filical point of view each of these would represent a "mon-angial sorus" of Prantl, and if the branch-system were dorsiventral the result might be such as is seen in the living *Botrychium* (Fig. 299, *D*, *E*). But in the great majority of the Ferns the telomes stand in trusses, or sori which are often radial while the cladode that bears them is dorsiventral. Nevertheless,

the position may be still distal, that is marginal on the flattened leaf, as in *Etaopteris* (Fig. 295); but the same type of sorus is borne superficially on the blade in *Ptychocarpus* (Fig. 301), or in the living *Gleichenia* (Figs. 345-6-8). In the more advanced Ferns there is a general tendency of the sorus towards the lower surface of the blade, and often it may be extended over a wide area of it. The details have been described in Chapters XVIII, XIX. The number of the sporangia may meanwhile be increased to indefinite figures, with a correlated reduction in the size of each, and in its output of spores. Thus, though in a general sense each sporangium may still represent the single capsule of a telome, strict identification is lost as the numbers increase by gradate sequence, or by interpolation: giving a striking illustration of a well-known principle noted by Darwin (*Origin of Species*, chap. v.).

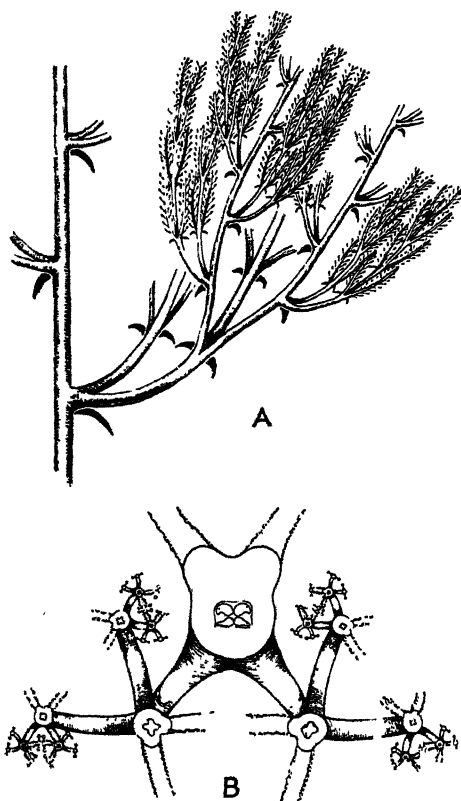


FIG. 448.

Stauropteris oldhamia, Binney. Diagrams after Hirmer. *A*=Branching of blade; aphlebiae at departure of the forking branches; on the parts of the spindle seen laterally only the visible aphlebiae are represented. Scale rather below natural size. *B*=Diagrammatic transverse section of the blade, constructed to show its branching. The aphlebiae are represented as minute circles.

It has been seen that enations of various type were borne laterally on the stalks of the Psilophytales, as well as on the stems of the more advanced Microphyllous Pteridophytes in which, as photosynthetic microphylls, they take a prominent place in the make-up of their vegetative and propagative tracts. In the Megaphyllous types also, whether early fossils such as *Ankyropteris* or modern Ferns, minor appendages appear of variable character,

such as hairs, scales, bristles, or spines. They are borne both on axis and cladode, and are most highly developed on the leaf-base and rhizome. They also occur in the fertile region, where specialised enations are described under the general term "indusium" (Chapter XXIX). All of these enations appear as sterile appendages on the "syn-telomes" of Zimmermann, whether in megaphyllous or in microphyllous types. Their differences lie in their size and structure; but particularly in their relation to photosynthesis and to the conducting system. Appendages of similar type have already been shown to be variable in these features among the primitive Psilophytales. The conclusion will then follow that *these minor appendages, however various and homoplastic, are all comparable in point of their mode of origin and their typical sterility, whether they be borne upon a megaphyllous or a microphyllous framework.*

Some readers will probably dissent from this conclusion, since it would rank under the general term "enation" parts apparently very different from one another. For instance, a ramentum, a photosynthetic microphyll, a bract-scale, and an indusium. But, in justification of this, attention must be fixed on the relation of the appendage to the part that bears it, rather than on its form or function. To take a special case, a comparison of the isolated marginal sporangium of *Lygodium* and its enveloping indusial flap (Figs. 304, B, 314), with the isolated sporangium of *Lycopodium* and its subtending microphyll is instructive (Fig. 183). In both cases a single telome is associated with a single enation, and in either case the supporting part is of "syn-telome" nature. A reference to Prantl's Schizaeaceae, Fig. 86, plate vi., and to his text, p. 43, shows that in *Lygodium* the sporangium lies "dorsally" on the vascular strand which is continued into the indusium itself. The relation, whether of position or of vascular supply, is in fact very closely similar to that of the relative organs in *Lycopodium*; and the origin of the parts is the same in both examples. *The chief difference lies in the symmetry of the parts that bear them:* in the Fern a dorsiventral and highly branched cladode, as against the radial and usually less freely branched strobilus of *Lycopodium*. It is, in fact, this difference of symmetry rather than of fundamental organisation that has determined the divergent course of evolution of the megaphyllous from the microphyllous Pteridophyta: and this is closely related to a difference in the incidence of photosynthetic nutrition on the framework of telomes that bear the enations.

Both types are foreshadowed in the shoot of *Asteroxylon* (Frontispiece). Its main branch-system, of syn-telome origin, forks distally: certain minor branches assume a lateral position, forecasting cladode-leaves; but the main axis bears also enations in the form of *Thursophyton*-leaves, forecasting microphylls. The upright shoots have radial symmetry, with occasional forking. If this were maintained the framework might readily lead to a microphyllous shoot, with projecting photosynthetic appendages, borne on an

axis not specially developed for that function : as in such types as the Lycopods, Sphenophylls, or Equiseta. If, however, the lateral branches of the framework were developed in a strongly dorsiventral manner, and the branchlets became webbed, very efficient photosynthetic blades would result from them alone, while the minor appendages would appear as protective ramenta, indusia, etc. This is apparently the key to the formal divergence of the microphyllous from the megaphyllous shoot. *Both have involved enations as well as telomes. But the function of photosynthesis has fallen in the one case on the enation-leaf, giving microphylls ; in the other on the syn-telome, giving a cladode-leaf bearing colourless ramenta. The difference is in symmetry, and in localisation of photosynthesis. It does not point to any essential difference of primary organisation, which is in both based upon telomes and enations (Principle V.).*

There remain certain enigmatical parts which have been described as "Aphlebiae." Two quite distinct types of appendage borne upon the rachis of Ferns have been included under this title. In certain living Ferns some of the lower pinnae differ from the rest in outline and texture. In *Hemitelia capensis* and some other Cyatheoids these are found near to the base of the leaf-stalk : comparison shows that they are, by position and structure, of the nature of pinnae, arrested and specialised ; but they are left in a basal position owing to localisation of intercalary growth above rather than below their insertion.¹ There is no question here but that they are of pinna-nature. But occasionally whole cladode-leaves may be subject to a like change : for instance in *Trichomanes aphlebioides* Christ, recently examined in detail by Dr. Williams.² Here the first fronds of the axillary branches are modified so as to resemble the aphlebioid pinnae of *Hemitelia capensis*.

In various fossils, both Ferns and Pteridosperms, other appendages are found that do not correspond in position to pinnae. There is no need to quote a number of examples, but rather to summarise the recent results of Holden, who has given more accurate details for *Ankyropteris corrugata* than any which have hitherto been published.³ The parts styled here "aphlebiae" are borne as flattened scales both on stem and leaf. They are closely set on the axis, but on the leaf they are in alternating series on either flank. In Zygopterids generally their disposition shows considerable variety.⁴ They are lobed, and are traversed by vascular strands which spring from the vascular tracts of stem or petiole, and fork to supply the lobes, which are of variable size. They are firm in texture, but with intercellular spaces ; they have perhaps a ventilating function, and are protective of the other parts while young, in which felted hairs also bear their part. In addition the stem and leaf-bases bear hispid hairs. As to the homology of these aphlebiae with other parts the presence of a vascular supply is not itself distinctive in face of the facts known for the appendages of the Psilophytales (Fig. 425). They do not appear to be of telomatous nature. Most probably they are comparable with enations, or

¹ See Bower, Studies II., *Annals of Bot.*, vol. xxvi., p. 294, plate xxxiii.

² *Proc. R.S. Edin.*, vol. I. (1930), p. 142.

³ *Phil. Trans.*, B., vol. 218, p. 93.

⁴ Holden, *l.c.*, p. 104.

Thursophyton-leaves, here advanced in structure; and their position upon axis and cladode would accord with that view. But, as regards the absence of photosynthetic tissues, they would be best ranked with the protective ramenta, often of large size though not vascular, borne upon living Ferns, such as the *Cyatheaceæ*.

PARTS OF INDETERMINATE CHARACTER

A certain degree of success has been reached in the foregoing pages in the resolution of the varied organisation of the sporophyte present in the Archegoniatae, in terms common for them all. It is due to the use of wide definitions, combined with a free recognition of homoplasy. It must not be assumed that all parts of primitive plants should necessarily fall into standardised categories such as have been based upon experience of the higher plants, though they may do so up to a point; but special parts may exist that cannot be so ranked, being of indeterminate character. To those who adopt an upward evolutionary outlook the Archegoniatae will suggest an experimental stage in which false starts and temporary makeshifts should be expected. This view may be illustrated by a few examples.

I. The swollen embryonic stocks of Lycopods called "protocorms" have been discussed at length in Chapter XIV. Treub believed that they represent an ancient feature of phylogenetic importance, appearing as a rootless body bearing protophylls; that this passed over later to the normal leafy shoot, and that it figured historically in the establishment of the rooted sporophyte. Notwithstanding the presence of a tuberous stage in some of the Psilophytales, tuberisation may be held as a secondary and sporadic rather than a general embryonic feature. Its biological importance where it actually exists was probably to collect reserve material to be used later in feeding the definitive shoot. Wide comparison of the embryology in the Lycopodiales indicates the type seen in *L. Selago*, where there is no protocorm, as fundamental (Figs. 208-9); and the protocormous types take their place as biological betterments upon it, that meet special conditions (Figs. 213, 215). There seems no justification for according to them phylogenetic importance, notwithstanding that in extreme cases they profoundly alter the normally obconical form of the embryo (Fig. 214).

II. The adult sword-shaped leaves of *Tmesipteris* have been described in Chapters VII and XXVII. The first leaves of the sub-aerial shoot resemble the simple leaves of *Psilotum*, but they pass gradually to the compressed adult form, bearing a distal "mucro." Comparison with *Psilotum* shows that this is the original enation which is borne up in *Tmesipteris* on an intercalated zone, fully equipped with stomata and a vascular strand, of intermediate nature between axis and enation-leaf. (Figs. 84, 85, 90 bis.)

III. The roots of the Lycopodiales frequently spring not directly from the stem but from intermediate growths described respectively as rhizophores in *Selaginella* (Fig. 158), or as Stigmarian trunks in the Lepidodendroid fossils (Fig. 159); while in *Isoetes* and *Pleuromoia* (Fig. 160) their relation to the stock may best be understood as presenting the Lepidodendroid base in a greatly condensed form. It is difficult to rank these parts genetically or

structurally within the categories of formal morphology. Probably they may all be referred in origin to rootless plants with subterranean leafless rhizomes, such as the Psilophytales. Absorptive roots originated upon these as new organs; hence they are fitly termed "rhizophores." In *Isoetes* and *Pleuromia* they have been subject to considerable further evolution, resulting in the peculiar conformation which the bases of these plants show, and they are referable neither to typical axes nor to typical roots.¹

Such examples will suffice to illustrate the experimental character of Archegoniate vegetation; but they present peculiar difficulties to those who uphold definite categories of the members composing the shoot.

EMBRYOLOGICAL EVIDENCE BEARING ON THE TELOME THEORY

Each Bryophyte sporogonium may be held as a simple Telome, representing the sporophytic shoot in a rudimentary form. Its simple embryology gives a basis for comparison with those more elaborate mouldings which precede the establishment of a Pteridophyte Plant (Figs. 406-410). It has been seen in Chapter XXVI that, in all fully investigated cases, the apex of the shoot bears a definite relation to the first cell-cleavage of the zygote, appearing as nearly as possible at the centre of the epibasal hemisphere; while leaves, roots, and suctorial organs follow as lateral developments on the *primitive spindle* defined on the one hand by that apex and on the other by the basal suspensor where present. In this early definition of polarity the embryos of vascular plants correspond to the sporogonia of Bryophytes. The further question then arises what evidence does embryology afford in the establishment of the further organisation based on telomes and enations, developed respectively in megaphyllous and microphyllous types. It must not be expected that such evidence will be explicit, for the several types of embryo develop under conditions substantially alike for them all. All Archegoniate embryos are encapsulated at first: hence a certain degree of similarity may be anticipated before the definitive form of the adult shoot is reached.

There is no known embryology of the Pteridophyte fossils; but the forking shoot of *Rhynia* suggests an origin by dichotomy of a simple Moss-like spindle. If that forking were repeated with unequal development of the shanks, a common stem of dichopodial type would result; while sterility of certain branches, others retaining their fertility, would result in the adult state of the simplest known types of Pteridophyte (Figs. 78, 79). If distally this axis showed only vegetative apical growth, while the minor shanks retain their forking and ultimate fertility, the result would be a megaphyllous shoot consisting of a predominant axis bearing lateral sporophylls. This is all foreshadowed in *Rhynia*, and exemplified more fully in *Asteroxylon*, or in the

¹ Weiss, Pres. Address, *Linn. Soc. Proc.*, 1931, p. 151.

habit of simple Ferns. The only embryology available for comparison among rudimentary types of Vascular Plants is that of *Tmesipteris*, with its forking but leafless primary shoot. Sometimes it presents an early dichotomy (Fig. 449). If one of these shanks of dichotomy were consistently sterile and repeatedly branched, while the other were side-tracked and remained fertile, this would prefigure in terms of Psilophytales and Psilotaes the axis and cladode leaves of the *Megaphyllous Pteridophytes*. The embryology of



FIG. 449.

Tmesipteris: photograph of the forward end of a prothallus, showing a young laterally attached plantlet with two apices. Compare Fig. 429. (After Holloway.)

Helminthostachys, which is held by many to be a very primitive Filical type, is compatible with this view based upon the forking embryo of *Tmesipteris*. The upright hypocotyl supports the cotyledon and the continuing bud (Fig. 384, B). Their relative positions accord with a dichotomous origin, with dichopodial forking already a pronounced feature, to be repeated as the next cladode leaf develops. In the hypobasal hemisphere the first root originates laterally. The advance on what is seen in *Tmesipteris* is such as might have been anticipated, while the facts for *Helminthostachys* support the reading of the embryo of Leptosporangiate Ferns already offered in Chapters XX and XXVI. If that comparison holds, then for Ferns at large it may be concluded that the epibasal hemisphere of the Fern-embryo forks at once, like certain embryos of *Tmesipteris* (Figs. 416, 429): the one shank giving rise to the

axis, the other to the first cladode leaf. Either of these may bear enations, but only the latter is directly fertile.

Among the *Microphyllous Types* the early stages in establishment of the axis appear simpler than this, particularly in the Articulatae. The only known example of Articulate embryology is that of *Equisetum* (Chapter X, Fig. 147, also Fig. 427). Here the polarity is exoscopic, and the apex with its regular segmentation is defined by the first and immediately succeeding cleavages, being central in the epibasal hemisphere. The leaf-sheaths appear as circular enations below the apex, which itself leads directly to the first shoot. Apart from the successive leaf-sheaths and the obliquely lateral first root the embryo is an abbreviated primitive spindle, comparable with that of a Bryophyte (Chapter XXVI). This embryology is consistent with a reading of the Equisetoid plant as primarily a telome, with frills of enation-leaves or microphylls all of lateral origin, and continued after various branchings to a *Hostimella*-region where the telome twigs are condensed to the form of sporangiophores. What the organogenic relation of the sporangiophores may have been to the primitive spindle, in this and other Articulatae, is not yet clear; but it is broadly suggested by *Asteroxylon*, and it may be revealed later by further study of early fossils. A reasonable working hypothesis would be that from a distal *Hostimella*-region, developed sympodially, a relative main axis with lateral telome-trusses would emerge, to be condensed later into sporangiophores borne on a sterile axis. This would involve starting from a type such as is actually seen in *Asteroxylon*.

The embryo of *Equisetum* shows that, in a microphyllous sporeling, the enation-leaves may appear at points lower on the primary telome-stalk than in the Psilotales and Psilophytales, and consequently the naked base is short. But from the first the apex of the axis in the *Equisetum* embryo is clearly in advance of them (Fig. 147). In the embryo of the Lycopods, however, as seen in *Lycopodium Selago* (Fig. 208) or in *Selaginella spinulosa* (Fig. 219), the first leaves of the embryo overshadow it. But even here the apex holds the same place at the centre of the epibasal hemisphere as in *Equisetum*; therefore the microphylls are from the first lateral, though the apex is apt to be thrust aside by the first leaf. This appears to be due to the precocious development and disproportionate size of these first *Thursophyton*-leaves. The axis that bears them, together with the hypocotyl, represents the stalk of the initial telome (Figs. 208, 209). Subsequently dichotomous branching of that axis in primitive types, though with gradual dichopodial steps towards monopodial branching in those that are more advanced, gives the system of stems seen in the Lycopods. In all but the most primitive types the microphylls have spread also distally into the fertile region to form the composite strobilus. The general result is that these enations, which are absent from the simplest Rhyniaceae, localised in *Asteroxylon*, and wanting from the base of the plant in the Psilotales, may appear by anticipation, as prominent objects in

the early embryonic stages of Lycopods and Equiseta, and extend throughout the sterile shoot.¹ On the other hand, while they are absent from the *Hostiella*-twigs of *Asteroxylon*, and from the cones of *Zosterophyllum*, *Archaeocalamites*, and *Equisetum*, they accompany the sporangia and sporangio-phores in the cones of Lycopods, Calamarians, and Sphenophylls, giving the composite strobili already discussed. It thus appears that the facts of embryology may be interpreted in terms of the adult shoot, whether in megaphyllous or in microphyllous types.

It remains to review the bases of plants so constructed, and the attachment to the sources of supply. In all the Archegoniatae the prothallus feeds the embryo in the first instance, and in varying degree the base of the spindle is adapted accordingly. Connection is maintained with the maternal tissue by haustorial developments varying in size, form, and position, but transitory in function: these are included under the name "foot." In *Anthoceros* and *Tmesipteris* the receptive surface is increased by rhizoid-like processes (Figs. 6, 100). In the former this is final, but in the latter it is only temporary, the basal region being at last disorganised; the sporeling of *Tmesipteris* then acquires its supply from the soil saprophytically, by aid of a symbiotic fungus. Finally, the aerial shoots emerge above ground; but there is no root-formation, and this appears to have been so also in *Rhynia* and *Asteroxylon*. In rooting organisms, such as the primitive *Selago*-type of *Lycopodium*, or in *Equisetum* and in the Ferns, the base of the spindle is not specially modified on transition from dependence to independent establishment in the soil. But in not a few ancient types there are anomalous developments, usually related to mycorrhizic nutrition and storage of material, grouped under the term "protocorm." They may be recognised as occasional adaptations to meet the difficulties of youth (Chapters XIV, XXVI). Apart from them the primitive spindle stands as the initial type of the archegoniate embryo. As for the roots, *their origin is always lateral on the spindle*, and usually endogenous. But the first root of the embryo in *Lycopodium* and *Phylloglossum* is exogenous, a fact that suggests that the endogenous origin seen later may not have been really primitive.

The cumulative result of analysis of the sporophyte in Archegoniate Plants is to trace all its varied forms back, ontogenetically or by comparison,

¹ See footnote on "Prolepsis," p. 556. In the present discussion anticipatory development of enations is suggested by comparison of *Asteroxylon* or *Tmesipteris* with the embryos of Lycopods and Equiseta. In the former the appendages appear late in the individual development, in the latter they follow close on the definition of polarity in the embryo. Comparison suggests that their distribution has been extended downwards by anticipation. Conversely, in the theoretical treatment of the cones of *Lycopodium* and *Calamostachys*, the distribution of the enations as bracts, upwards so as to invade the cone, has been contemplated as the most probable solution of the relation of bracts to sporangia or sporangio-phores, as compared with the bractless state of *Zosterophyllum* or *Equisetum*. The underlying idea of anticipated or of deferred development of appendages is thus not a novel one.

to simple beginnings. Ultimately the *telome* underlies them all, though subsidiary *enations* appear as secondary amendments added in the more elaborate types. The simplest example as regards form is seen in the Bryophyte sporogonium. Here we find, even in the most elaborate capsules, merely the result of working out the organographic unit into high specialisation. This makes itself apparent also in the first steps of other Archegoniate embryos as a *primitive spindle*, with its apex consistently central in the epibasal hemisphere, while its base is represented by the suspensor when present (Chapter XXVI). If we enquire what has been the origin of this embryonic spindle, we encounter once more the problem of its encapsulation within the archegonium, which Von Goebel has rightly described as an "academic" question, because there is as yet no exact explanation of its source, though its existence is a general fact of observation in land-living plants. Is the spindle-form due to an originally free sporophyte of some non-encapsulated Alga, with polarity already defined in relation to a fixed substratum; or does some moulding influence by the archegonial venter determine it? Perhaps both factors contribute towards bringing about and maintaining the form of this ultimate sporophytic unit of land-vegetation. It may be designated either the *primitive spindle* when speaking in terms of embryology, or the *primary telome* in the analysis of the adult. The former term, introduced into embryology in 1922, connotes the organographic unit in the embryonic state; the latter, introduced by Zimmermann in 1930, is applied to the adult fertile unit. Assuming the validity of the foregoing analysis, *the primitive spindle of the embryologist would represent the primary telome itself.*

CHAPTER XXXI

SUMMARY OF RESULTS, AND EPILOGUE

THE chief object of this work has not been to trace phyletic relations between Archegoniate Plants ; though those who will may be interested to use the data here supplied in that way. It has rather been by examining them comparatively, to visualise the Methods of Advance which these primitive Land-Plants appear to have followed in their evolution. The primary source of evidence has been the study of the living Archegoniatae ; but the reasoning based on these has been checked by reference to palaeontological facts. This mode of enquiry should lead to more valuable results in the organographic study of Land-Plants at large than any mere search for phyletic schemes.

Alternation of Generations, as demonstrated by Hofmeister for the "Higher Cryptogamia," has formed the foundation for this study of Archegoniate Plants. Since his time it has been proved to be constant as the normal cycle of events for all groups of living Archegoniatae, and there is reason to believe that it held also for correlative types now known only as fossils. The demonstration that the alternating phases differed in nuclear construction came gradually and culminated in Strasburger's recognition of the Periodic Reduction, in 1894. The two phases were thus correlated in their inception with the alternating events of *Syngamy*, involving nuclear fusion and *doubling* of the number of chromosomes ; and of *Meiosis* or *Reduction*, an event which is the usual prelude to spore-formation. This normal succession of events in any completed sexual cycle may be represented diagrammatically as in Fig. 2. The alternating somatic phases take their places in this scheme as the *haploid gametophyte* intervening between the events of meiosis and syngamy, and the *diploid sporophyte* between syngamy and reduction. Such a scheme, underlying as it does the life-history of normally developed Archegoniate Plants, and stabilised by the biological advantages which it brings to organisms of amphibial habit, is the natural starting point for their organographic treatment, whether from the comparative or from the evolutionary point of view (Chapters XXIV and XXX).

The Archegoniatae hold a middle position in the whole scale of vegetation, between the Thallophytes and the Seed-Plants. This suggests comparisons downwards and upwards. An early assumption was that they, being essentially Land-Plants though somewhat amphibial in their habit, were descended from an Algal ancestry, such as is seen living to-day ; and that they, on the

other hand, gave rise to the Seed-Plants as we now see them. Both these assumptions, which were natural products of post-Darwinian enthusiasm, require to be carefully considered before they are adopted for purposes of general comparison. The former assumption, that the Archegoniatae were descended from Algae resembling those now living, seemed to be supported by the demonstration that the life-history of many of these has also been found to include two alternating phases, cytologically haploid and diploid. This fact has been critically evaluated as evidence by Oltmanns, who suggests that there has been a homoplastic origin of the sporophyte along a plurality of lines. Von Goebel, following a similar line of thought, finds it impossible to bring any one family of living Thallophytes into genetic relation with the Archegoniatae, and concludes that the doctrine of alternation founded originally for the higher plants—from the Bryophytes upwards—cannot be extended to all plants. If this be so, the conclusion will follow that the alternation of generations seen in the Archegoniatae will have to be discussed as an independent proposition. *The general view here adopted is that homoplastic post-sexual-phases have been developed independently in widely different evolutionary lines*: in which case such similarity as the Algal sporophyte bears to that of the Archegoniatae would probably be homoplastic rather than truly homogenetic. On the other hand, the question of their relation to the Gymnosperms may be accepted as Hofmeister left it, though the evidence is now amplified by a great volume of added fact, viz., that “the embryo-sac of the Coniferae may be looked upon as a spore remaining enclosed in its sporangium: the prothallium which it forms does not come to light.”¹ The further application of this conclusion to the Angiosperms, and the evolutionary continuity which it implies, may be left for decision as better knowledge of the early fossil Seed-Plants comes to hand. The result will therefore be that the Archegoniatae, while they appear as fore-runners of a more advanced Land-Vegetation, stand aloof from any known Thallophytic origin, unless there be some remote connection with Isokont Green Algae. They will be best studied as an independent evolutionary innovation on land, rather than as a direct extension of a Thallophytic Flora from aquatic to sub-aerial habit. The fact that their most characteristic feature, the archegonium, is throughout highly standardised in relation to an internal embryology so necessary for life on land, confirms this as a correct attitude of enquiry for them.

Taking then the normal nuclear cycle as the starting point for somatic development in the Archegoniatae, the immediate problem will be the origin in relation to it of their alternating somatic phases. It seems probable that the nursing gametophyte preceded the embryonic sporophyte dependent upon it; and this probability is strengthened by the existence of many Algae which are haplobiontic, their single soma being haploid. In them the sporo-

¹ *Higher Cryptogamia*, p. 438.

phyte is represented only by the zygote, in which reduction follows in its first nuclear division. *Such data form a basis of fact for the theory of interpolation, which is here adopted for the Archegoniatae.* The initial steps of interpolation of the sporophyte between the events of syngamy and reduction are not illustrated by any series of living Archegoniate Plants; nor is it likely that they should be if the interpolation of a soma were as important a biological event in the establishment of land-vegetation as its constancy shows it to have been. The earliest steps would probably be eliminated in the rush for higher successes. But they may be inferred on the one hand from the comparison of simple Algae, such as the Green Isokonts, and from the ontogeny of the embryo on the other. *The first essential would involve a delay of meiosis by sterilisation, the first divisions resulting in vegetative tissue, though leading finally to spore-formation.* This would be in accordance with Naegeli's fundamental law of organic development. The result as actually seen in living Archegoniatae, even in the simplest of them, is the normal alternating scheme fully established, with its gametes and its spore-mother-cells punctuating the limits between the probably prior haploid phase, and the probably later and interpolated diploid phase.

Either of these phases once established is capable of indefinite further vegetative development, with increase in size and variable capacity for self-nutrition. If the history of them has been as here suggested the two phases would not be strictly homogenetic, but so far as any similarity of contour or character appears it would be homoplastic, notwithstanding that they are phases of the same life-cycle. From this point of view they may be compared, with the anticipation that their organisation will show some degree of similarity, though open to essential differences of detail. Thus, however intimately related one to another, *the two phases would be separate organogenic propositions: the one normally with a haploid, the other with a diploid cytological constitution.*

In following out the progress of either phase, whether from the ontogenetic or the evolutionary aspect, certain principles should be adopted: (1) to maintain an upward rather than a downward outlook in the comparative analysis of plant-form, with (2) a preference for normal over abnormal or occasional features. (3) It should be realised that homoplasia has been a frequent phenomenon in evolution, while homology in the strict sense is less common than is usually assumed. (4) The distinction should be recognised between distal forking and enation as methods of increase in number of parts: it is indeed fundamental in the development of the primitive sporophyte, though that distinction cannot be strictly maintained in later derivative types. (5) The incidence of photosynthesis is variable, but its effect is to mould not to originate parts. Not only may a photosynthetic part lose that function, but also photosynthesis may be established in a part originally colourless. (6) It should also be realised that distal fertility in primitive

forms is consequent upon the priority of demand for nutrition over propagation ; and (7) that the factor of size is the most constant and inevitable of those conditions which influence the form of the growing biont, whether diploid or haploid. Each of these principles has been discussed in Chapter XXX. Their observance is essential for a correct outlook upon evolutionary problems relating to either of the alternating phases ; but particularly to the nascent sporophyte, the behaviour of which in the Archegoniatae illuminates the morphology of all the Higher Plants. The upward outlook is specially essential to correct the mistaken results of the old Nature Philosophy. It works out in the interpretation of the higher results of evolution in terms of the lower, and not the converse.

Comparison within the Bryophyta may point to general features that are ancestral for the Archegoniatae. In this the Anthocerotales stand out as providing structural clues. The alternating phases are here more alike than in other Archegoniatae ; both are photosynthetic, with stomata structurally efficient in the diploid, but only imperfectly suggested in the haploid phase. As Von Goebel points out (*l.c.*, p. 676), the latter appears only secondarily (*erst nachträglich*) to have assumed an hygrophytic structure. Both gametophyte and sporophyte are, however, sub-aerial and photosynthetic : probably they were also both originally upright, and cylindrical. The former has no specialised grouping of the gametangia, while the latter shows less differentiation of its vegetative and propagative regions than is seen in any other Bryophyte. *The inference is that in the Anthocerotales we see a very primitive type of Bryophyte in which both phases represent an Archegoniate vegetation of an early and synthetic type.* Nevertheless, the relation of the alternating phases in the Anthocerotales is that usual for the Archegoniatae at large : they give no answer to the problem of encapsulation of the embryo within the maternal tissue, which is so characteristic a feature of the Archegoniatae. It is thus impossible to do more than surmise whether or not in still more primitive land-plants fertilisation may have been originally free in water, as in most Algae, and that the diploid plant itself may have been independent at the first. On these points living plants of the land are dumb.

The inward urge towards increase of Size, with its attendant elaboration of primary Form and of Structure which is inherent in all vegetation, may take effect in both of the alternating phases ; or independently in either of them. The known types of the Archegoniatae illustrate this with divergent results, respectively, in the Bryophytes with their dominant haploid phase, and in the Pteridophytes in which the diplophase is dominant. A brief comparative summary of the leading features of the gametophyte and of the sporophyte from the point of view thus sketched will be useful in drawing to a conclusion this organographic study of the Archegoniatae.

THE ENLARGING GAMETOPHYTE

The *gametophyte* of the Anthocerotales, like the prothalli of most Ferns, is flattened and photosynthetic, but without appendages excepting occasional and irregular lobes. It is endowed with apical growth and branching, but it has no system of effective internal ventilation, notwithstanding the occasional presence of mucilage-slits, which appear to represent vestigial stomata. A due proportion of external surface to bulk is, however, attained by the very simple means of flattened form and branching; and it is greatly in advance of that of a cylinder of equal volume. These remarks apply also to the majority of Fern prothalli, and to certain flattened protonemal developments of *Sphagnum*, *Tetraphis*, etc. But in other Bryophytes the adjustment of surface to increasing bulk is secured by elaboration of form along either of two divergent lines. In the Marchantiales there is *internal ventilation* of the fleshy thallus, the complex surfaces that line their cavities communicating by stomata with the air outside. But in the leafy Jungermanniales and in the Mosses there is *foliar development*, which produces a like result by elaboration of the *outer* surface. *The remarkable fact is, however, that in the gametophyte these methods are alternative; and no Bryophyte has combined them in the somatic development of its haploid phase, after the manner of their own sporophyte, or of land-vegetation at large. This probably accounts for the limited size of the haploid phase.*

In the Pteridophytes, where the prothallus is often large and fleshy, the combination of elaborated form with internal ventilation is again absent. In some few large prothalli that are photosynthetic there may be a few irregular leaf-like lobes, which provide an extended external surface as the bulk increases upwards; for instance, in *Equisetum* or *Lycopodium cernuum*. These may be held as concessions to a demand for increased presentation-surface in photosynthesis. But the saprophytic prothalli of *Tmesipteris*, and *Lycopodium*, and of the Ophioglossaceae, are without either ventilation or elaboration of form. Excepting the Algae, they are among the largest known masses of unventilated living plant-tissue of simple form, and consequently of low presentation-surface. The suggestion has been made that either slow diffusion in the liquid in which the mycorrhizic tissues are bathed may make up for deficiency of surface, or that the presence of oxidases may provide an increased oxidising mechanism (Chapter XXV). Whatever the explanation may be the fact remains that certain plants of ancient type have survived (and possibly a sluggish saprophytic metabolism may have contributed to that end) notwithstanding the simple form and unventilated structure of their prothalli. The limited dimensions of the gametophyte in the Pteridophyta also may be attributed in part to a want of driving-power of the haploid phase: but the fact that the combination of complex external

form with internal ventilation, which is characteristic of the successful diploid phase on land, is here absent has probably itself been a potent factor in determining its stunted growth.

Here the gametophyte may be left aside, since it takes only a minor part in the origin of land vegetation, becoming finally a mere vestige. It is the sporophyte which takes the lead, and establishes a final ascendancy in the Vegetation of the Land. Nevertheless, such a feature as the obconical form is in the first instance common to both phases, and brings in its train structural consequences that are alike, though homoplastic. The most obvious of these is foliar development.

THE ADVANCING SPOROPHYTE

It has been seen in Chapter XXX how the Archegoniate Sporophyte may be analysed as composed of (1) *Telomes*, each consisting of a stalk, usually with vascular supply, and a distal sporangium; (2) *Enations*, which do not normally bear sporangia: this term covers hairs, scales, spines and microphylls; (3) *Roots*; and (4) occasional *organs of indeterminate character*. The Telome is the original source of these, a conclusion which accords with the structure of the simplest examples, as well as with the facts of embryology. It cannot be expected that in organisms so varied, and in evolutionary lines so distinct as those comprised in the Archegoniatae, the analysis could be carried out completely, or the detail of derivation fully explained; for in the simplest examples we are presented with the fact of alternation already established, with a sporophyte in being. Here it must suffice to summarise briefly the main facts, and to show how they accord with the general results of this analysis.

Comparison of the sporogonia in the Bryophytes indicates those of the Anthocerotales and Sphagnales as alike in certain primitive features. As in the Bryophyta generally, each may be held as a simple telome without appendages, but with imperfect differentiation of the vegetative and propagative regions. They form a synthetic bridge between Liverworts and Mosses not only in these points but also in the details of their sexual organs (Chapter IV). They suggest as a relatively primitive state *an unbranched spindle with exoscopic polarity, diffuse rather than localised photosynthesis, and with internal spore-production*. These may be accepted as features underlying the sporogonium of Bryophytes generally, while the more highly specialised capsules of Liverworts and Mosses, as compared in Chapter VI, may be held as variants upon the imperfectly differentiated telomes thus presented. Instances have from time to time been recorded of branching of sporogonia (Fig. 440); but there is no evidence of this having become a stable feature of any race of the Bryophyta. And so the matter stood till the discoveries at Rörägen, Rhynie, and the Rhine Valley. These have presented an early

Devonian vegetation based on forking of a sporophyte that offered ready analogies in other respects with those Bryophytes that are regarded as primitive ; and particularly with the Anthocerotales.

Assuming for purposes of comparison some evolutionary connection with the Bryophyta, these plants show the following advantageous innovations : (1) physiological independence ; (2) forked branching ; (3) dichopodial development ; (4) a definite conducting tract ; (5) enations ; and finally (6) continued apical growth, often with circinate vernation. But still there is an absence of the definition of axis, cladode leaf, or root ; and in this respect the organisation of these plants is still rudimentary. On the other hand, they share with sporogonia the stomata and internal ventilation so necessary for photosynthesis in any elaborated sub-aerial part. The smaller types of *Rhynia* and *Hornea* illustrate 1, 2, 3, and 4, as their salient features ; it is only in the larger *Asteroxylon* that 5 and 6 are fully established. The formation of "*Thursophyton*" leaves, and the presence of a conducting tract moulded into flanges, do not appear in its smaller twigs, but in those of larger size. Thus elaboration of form, whether external or internal, appears to be correlated here with the size of the organism, or of that part that shows those features. This is believed to be not a matter of chance, but probably of causality. The greater complexity appears in the larger plants of the same type and geological age as the smaller. These most archaic vascular plants provide perhaps the best, as they are also among the earliest examples of elaboration of primary form of the sporophyte in relation to increasing size : a relation which pervades further evolution, though without exact numerical proportion, and often disguised or superseded by secondary changes.

These early Devonian Plants thus form a synthetic bridge, whether in respect of external form or of internal structure, between the simple telomes of the Bryophytes and the more complex and commonly larger sporophytes of vascular plants. The result of their innovations is a self-dependent vascular plant capable of indefinite enlargement without undue loss of proportion of surface to bulk, whether external or internal.

The simple shoot of *Rhynia* or *Hornea* suggests an origin by bifurcation from a single telome, with the capsule-formation delayed. That of *Asteroxylon*, though the largest and most elaborate, may be analysed, as regards its main trunks and its minor twigs, as springing also by bifurcation of an original telome (Frontispiece). But here dichopodial development and delay of fructification result in a branch-system that clearly foreshadows either cladode leaves bearing sporangia distally, or a truss of fertile twigs liable to condensation into a strobilus. Thus it is synthetic between the megaphyllous and the microphyllous types of organisation. To achieve the former, dichopodial side-tracking of fertile branches, developed bifacially in relation to a relative axis while the main trunk continued indefinitely sterile, would produce a shoot of Fern-like type with axis and cladode leaves.

A similar dichopodial development, with the fertile branches retaining their radial habit and each terminating in a single capsule, would give the type of *Zosterophyllum* and of the Lycopods ; or if each bore a truss of capsules it would give such sporangiophoric types as the Psilotales, Sphenophyllales, and Equisetales. All these results of evolutionary progress would thus be based upon forking of telomes, each with a potential, though possibly delayed or abortive, distal capsule.

But many of the Psilophytales, such as *Psilophyton* and *Arthrostigma*, and in particular *Asteroxylon*, possess minor appendages that arise not by distal forking but by outgrowth from surfaces not previously occupied. Similar developments are present in other Classes of Pteridophytes, and they are here collectively included under the general name of *Enations*. They appear as accessory growths upon the essential framework of telomes, or their direct derivatives. They vary in size and character, taking the form of hairs, scales, or spines ; or they may show photosynthetic development with various degrees of vascular supply. They may even attain a full development as microphylls, with stomata, mesophyll, and a vascular strand. Collectively they are not to be regarded as reduced, but as rudimentary parts that have been caught on an upgrade of evolution, which culminates in the photosynthetic microphyll. The "*Thursophyton*" leaves of *Asteroxylon* take a middle position, being photosynthetic, each with its own leaf-trace that stops short at its base (Fig. 425). Though the microphylls are absent from the smallest *Hostimella*-twigs of *Asteroxylon*, on the main shoots they extend up to the circinate tip, giving the habit as of a Fern-cladode with its ramenta (Frontispiece). This comparison is believed to be a valid one, and it receives support in the presence of minor appendages of like nature in Coenopterid Ferns. Doubtless the minor appendages, ranked as Enations according to their superficial origin and their normal sterility, are widely homoplastic. They are all complementary to the telome-framework, and occur particularly where it is of robust type. Their distribution accords with this view, particularly their absence from the basal region in *Asteroxylon* and in the living Psilotales ; and their gradual enlargement upwards from the point where they first appear.

Distally the fertile twigs in certain ancient types may bear no enations, only sporangia or sporangiophores, as in *Asteroxylon*, *Zosterophyllum*, *Archaeocalamites*, and *Equisetum*. This is believed to present a relatively primitive state ; and where the branching is not diffuse, as it is in the *Hostimella* branches of *Asteroxylon*, but compact, the result is a bractless cone. Some of the most archaic fossils show lax types of cone, as, for instance, *Zosterophyllum* and *Hostimella racemosa*. Here it must suffice to refer to the extended argument in favour of the composite nature of the bracteate cone seen in many of the microphyllous types : it has been developed in Chapters XV, XXIX, and XXX. It has led to the conclusion that, in a plurality of types of

the strobiloid Pteridophytes, the association of bracts with the sporangia or sporangiophores of the archaic bractless types produced a secondary or derivative state: microphylls having spread upwards from a middle vegetative region, such as that of *Asteroxylon*, into the fertile region corresponding to its *Hostimella*-twigs. There they established that loose relation to the individual telomes, or their trusses, which is shown by many instances to be prevalent rather than exact. The "annulus" of *Equisetum* is regarded as a last whorl of enations before passing to its still pure *Hostimella*-region. In *Calamostachys*, as also in *Lycopodium* and other microphyllous types, the enations permeate the whole cone *which with very few exceptions retains a radial symmetry*.

Approaching the problem of origin of megaphyllous organisation, not only from the side of the Psilophytales where it is prefigured by the dichopodial forking of telomes, but also from that of recognised Fern-types, a certain similarity to the character of *Asteroxylon* is seen in *Stauropteris*, the fertile branchlets of which may readily be compared with its *Hostimella*-twigs. Both branchings are three-dimensional, and the sporangia solitary and distal, on photosynthetic stalks. If such a frond were limited to two dimensions—a very natural amendment in relation to a supporting axis—and if the grouping of the sporangia were condensed, the result might be such as actually appears in *Botrychium*, or *Ophioglossum*, with *Helminthostachys* holding an irregularly intermediate position. Even the ventral "spike" of the Family would connote an isolated relic of anteroposterior forking. The marginal stance of the sporangia seen in the Ophioglossaceae is retained in the Schizaeaceae and Osmundaceae, but with a marked tendency towards their insertion on the lower surface. In the last named, as also in *Botryopteris*, *Etapteris* and *Corynepteris*, the individual telomes are grouped into trusses, or sori; while in *Ptychocarpus*, as in the modern Marattiaceae, the trusses with more or less perfect fusion of the sporangia take a superficial position on the flattened blade. Such steps suggest a transition to ordinary types of living Ferns with their expanded blade, the origin of which by webbing of the forked telome-stalks has been traced in Chapters XVI, XVIII and XXVII. *In contrast to the prevalent radial symmetry of the fertile cones of the microphyllous types these megaphyllous cladodes are of dorsiventral symmetry.*

There remain, however, in the make-up of the vegetative system in Ferns, various minor growths, which appear as hairs, scales or ramenta, and spines, together with those varied protective growths which pass under the name of "indusium." These all arise as surface-growths of lateral origin, and they are sterile. They have already been considered in Chapter XXX. Thus the dorsiventral cladode-system produces enations bearing the same formal relation to its constituent telomes as do the leaves and bracts to the radial shoots and cones of the microphyllous types. *The difference between the two systems*

is one of symmetry rather than of organisation. Closely related to this is a difference in localisation of the photosynthetic equipment. In the Ferns photosynthesis is centred in the cladodes, which are highly branched to form the dorsiventral fronds, while their branchlets are webbed to form photosynthetic blades, upon which the ultimate telomes and telome-trusses are borne. The enations are here represented as hairs, spines,ramenta, and indusia which very rarely contain chlorophyll. *Thus in Ferns the burden of nutrition rests upon the telomes, especially on their webbed stalks, while the enations are sterile and protective. In the microphyllous types nutrition is located more especially in the enation-leaves; and it is these that form the chief photosynthetic equipment.* The Articulatae, however, take a middle position as shown in the Equisetales. In the early Horsetails, such as *Asterophyllites* and *Annularia*, and in the Sphenophyllales, the microphylls are expanded and photosynthetic; in the latter and in *Archaeocalamites* they may be branched, with forking veins, thus providing a considerable photosynthetic system. But in *Equisetum* they are represented only by leaf-sheaths, often chaffy in texture, while photosynthesis is carried on by the tissues of the stem. Such comparisons show how flexible may be the incidence of photosynthesis upon the morphological framework of telomes and enations. It is not this, however, but the place and mode of origin of the parts which is distinctive in morphological analysis. In point of position and origin it may be said that, *as the photosynthetic leaf is to the system of telomes in the microphyllous, so is the colourless scale or ramentum, or even the indusium, to the system of telomes of the megaphyllous Pteridophytes.* But that is not the equivalent of saying that these enations are homogenetic in the evolutionary sense. Wide homoplasmy underlies their origin. These comparisons may be carried one important step further, in relation to the spore-producing members themselves. *There is essential correspondence between the single sporangium (telome), or sporangio-phore (telome-truss) of the microphyllous types and the single sporangium, or the sorus of the primitive Simplicies among the Megaphyllous Ferns.* This has been pointed out in Chapters XXV and XXIX.

By proceeding thus upwards from early and rudimentary Pteridophytes the shoot may be referred to two fundamental constituents, viz., Telomes and Enations. The distinction between them is based on developmental and comparative data, and it is indicated within the circle of the ancient and primitive Psilophytales. These terms are used in a broad sense, untrammelled by reference to types of higher organisation. *The "telome" was pre-existent and it is primarily fertile,* as is shown by comparison of early types, such as *Hornea*, *Rhynia*, and *Zosterophyllum*. The priority of a spore-producing part accords with the interpolation-theory, the foundation of which is that the spore has been a constantly recurring event in each normally completed cycle throughout the descent of the Archegoniatae. *The term "enation" is here applied collectively to various accessory parts that emerge*

laterally, not distally, from the surfaces of the telome-system, and they are not normally fertile. They are not standardised in early types of land-vegetation; in particular, photosynthesis is not a prevalent, much less a constant feature, though in microphyllous types it may be centred in them, in which case they frequently possess a vascular supply. The initial causes leading to the origin of enations present a problem to which no full answer can be given. But it is probably related in some loose sense to increasing size of the part that bears them. This is certainly suggested by the relatively large *Asteroxylon* with its *Thursophyton*-leaves, as compared with the smaller and leafless Rhyniaceae.

As the detailed knowledge of early fossils progresses from a study of impressions and incrustations to that of structure "in the round," it may be found possible to analyse their shoots also in terms of telomes and enations more fully than at present. Thus far they seem to offer problems of organisation rather than to solve them. On the other hand, among Seed-Plants the Pteridosperms show an organisation so close to that of the Ferns that for long they were ranked with them. Even now in some instances the line of demarcation is not clear, awaiting further knowledge of their reproductive organs. A vivid glimpse into the possible elaboration of telome-construction in them has lately been given by Halle, in his memoir on the structure of certain Fossil Spore-bearing Organs believed to belong to Pteridosperms.¹ The analysis here used will apply equally for the Filicales or for them. As to the rest, it will become increasingly difficult the further the subjects of it are removed from the Archegoniatae themselves. As an example reference may be made to the question, already raised in the case of the Araucarieae, whether or not these Gymnosperms are referable to a Lycopodiaceous, that is, to a microphyllous source: as against the Cycadaceae, which are probably of Filicinean, that is, of megaphyllous origin.² A decision on this point would materially affect the problem of the phyletic unity of the Gymnosperms. But such difficulties should not form an obstacle to the acceptance of the present reasoning, which has been applied to the study of the simpler and earlier vegetation; nor should it affect the validity for them of the results which have followed. Those results as illustrated in the Filicales suggest—in this most coherent and continuous sequence of types which extends from the Devonian Period to the present day—how greatly the organisation of related plants may be transformed from that of the original sources.³ The Ferns have always been held as relatively primitive in character; even the most advanced of them. How much greater may we expect the transformation to be in modern Seed-Plants? If this argument be given its due weight the attitude of further scientific enquiry will be, not to

¹ *Kungl. Svenska Vetenskaps. Hand.*, Band 12, No. 6, 1933.

² Seward and Ford, *Phil. Trans.*, 1906, B., vol. 198, pp. 305-411.

³ Bower, *The Ferns*, vols. i-iii., Cambridge Press, 1923-1928.

discredit the results here obtained because they may not seem to accord with what has appeared later in evolution ; but rather to use the experience gained from simpler types as suggesting a valid method of analysis and comparison, even for those that take the highest places in the scale.

EPILOGUE

Here the purpose of the present work ends. Its aim has been to lay a foundation for the organographic treatment of Land Plants at large by intensive study of those that are primitive. The result has been to form a conception of the original constitution of the sporophytic shoot, and of the early evolution of its parts. It must be left for others to pursue this analysis upwards to the more advanced vegetation of the Land, with its multiplicity of types and their high specialisation. There we may expect to find the traces of early evolutionary steps disguised and overgrown by later adaptive change ; as is that of the Coenopterids in the highly elaborated organisation of the Leptosporangiate Ferns. But notwithstanding this, as affecting the vegetative system, the spore-producing parts from which theoretically the whole of that interpolated system originated, retain their character ; and of these the microsporangia show a degree of conservatism which links the whole organisation historically together more effectively than any other feature of Land Vegetation. We conclude that such sporangia are the correlatives of those of the Primitive Pteridophytes, and, finally, of the distal capsule of some simple type resembling that of the living Bryophytes.

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